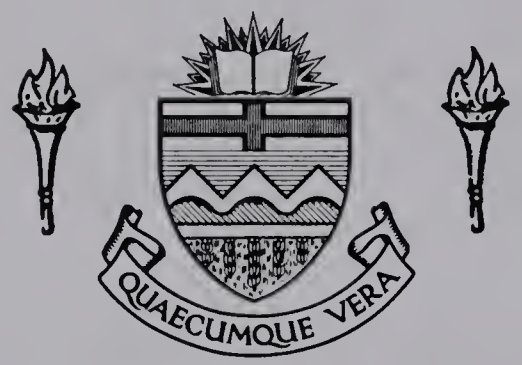

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CONTROLLED ENVIRONMENT STUDIES ON NET ASSIMILATION AND WATER RELATIONS OF ARCTIC *DRYAS INTEGRIFOLIA*

by

© ANTOINETTE P. HARTGERINK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Controlled Environment Studies on Net Assimilation and Water Relations of Arctic *Dryas integrifolia*" submitted by Antoinette P. Hartgerink in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Dryas integrifolia single attached leaves had maximum net assimilation rates of 18.7 mg g $^{1}hr^{-1}$ at optimum temperatures from 9° to 14°C. Positive assimilation could be maintained at temperatures between -5°C and +35°C , and at water potentials above a projected value between -20 and -30 bars. Light compensation was reached at 22.4 $\mu E\ m^{-2}sec^{-1}$ at 10°C. This value increased rapidly with higher temperatures. Dark respiration in non-dormant plants was high, but decreased as dormancy was approached. Photorespiration rates were low relative to dark respiration. The water potential (Ψ) could not be raised above -7 bars. Turgor pressure remained constant over a wide range of water potentials and water contents, which implies that *Dryas* has elastic cell walls. Leaf resistance remained constant at 5.6 sec cm ^{1} until a threshold Ψ of -18 bars (turgor ≃ 6 bars) was reached. Below this Ψ, leaf resistance was dependent on turgor pressure. The data led to the conclusion that water deficit must be the main limiting factor to net assimilation and growth of *Dryas integrifolia* on Devon Island.

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INTRODUCTION

Characterization of the photosynthetic response of a plant to individual environmental parameters is useful to promote an understanding of the pattern of that species' response to the sum of interrelated environmental aspects to which it is subjected in its natural habitat. An examination of this sort can best be carried out on individual leaves under controlled environment conditions in order to rule out as many unknown factors as possible.

During the course of the International Biological Programme tundra biome project on Devon Island, Northwest Territories, one of the studies was centered on the productivity and energy flow of a raised beach ridge community dominated by *Dryas integrifolia* M. Vahl.. In conjunction with this, the diurnal net assimilation response of entire *Dryas* plants was examined throughout the summers of 1971 and 1972 (Mayo, Despain and van Zinderen Bakker, 1973; Thompson, Mayo and Nelson, 1973). Some aspects of the water relations of *Dryas* in the field were examined by Addison (1973). This work provided the basis for a more detailed examination of the photosynthesis and water relations of *Dryas integrifolia* which was necessary to generate input for a process model of this species (Whitfield, 1973).

The aim of this study was to confirm and expand upon the information obtained by the field studies on *Dryas integrifolia* with respect to temperature, age, light and water relations of single leaves under controlled conditions.

MATERIALS AND METHODS

Growing Regime

Dryas integrifolia plants were collected from beach ridges on Devon Island during the 1972 and 1973 field seasons. The plants were potted in Edmonton, retaining as much of the original soil as possible around the roots and using greenhouse potting soil as a filler. They were fertilized with Hoaglands solution (Hoagland and Arnon, 1938), diluted 1:10 with water, before the start of each summer season. The plants were grown in controlled environment chambers (Environmental Growth Chambers, Chagrin Falls, Ohio) under the temperature and light regimes outlined in Table 1. Light was supplied by a mixture of 100 watt incandescent and warm white fluorescent lamps for which the spectral analysis is shown in Appendix B. Each simulated year consisted of 6 to 8 weeks of summer, 2 to 4 weeks of autumn and 1 to 6 months of winter conditions.

Gas Exchange

Equipment and General Method

The rate of net assimilation measured in the following experiments was taken to be the visible rate of uptake or efflux of CO_2 by the leaf in question. It can be defined as the difference between the rates of photosynthesis and respiration occurring in the tissue at the same time.

At various times throughout the summer season, the rate of net

Table 1. Characteristics of the controlled-environment regime under which *Dryas integrifolia* was grown in the laboratory.

Simulated Season	Time	*Light µE $m^{-2}sec^{-1}$ Hrs	Light Max	Light Min	Air Temperature °C Hrs	Air Temperature Max	Air Temperature Min	Comments
**1st summer	6-8 wks	24/0	200	-	24/0	10°	-	
**All other summers	6-8 wks, 7-9 days	15/9	150-200 (8000)	90-100 (5000)	-	10°	0°	Temperatures changed gradually, in 2 to 3° steps, several hours at each. Light changed abruptly. The two regimes were alternated.
	6-8 wks, 1-2 days	"	"	"	-	30°	0°	
**Autumn (dormancy induction)	2-4 wks	varies	90	0	-	+2°	-3°	Length of dark period gradually increased. Temperature changed slowly over 4 hours.
Winter	1-6 months	24/0	0	-	24/0	-2°	-6°	Covered with plastic bags and snow (when available) to prevent dessication.
Spring (breaking dormancy)	2-3 days	24/0	200	-	24/0	1-2°	-	Temperature changed abruptly, plants well watered and covered with plastic bags.

* Illumination in lux is included in brackets after the µE $m^{-2}sec^{-1}$ values. The latter were measured in photosynthetically active radiation (PAR) 400 to 700 nm.

** Plants were watered approximately once a week throughout the summer season.

** The onset of dormancy, as identified visually by a reddening of the leaves, was initiated spontaneously after 6 to 8 weeks of summer conditions, even before the plants were subjected to the hardening-off autumn regime.

assimilation of the plants in response to light intensity or to leaf temperature was examined by enclosing a single attached leaf (Fig. 1) into an open cuvette-gas analysis system (Šesták, Čatský and Jarvis, 1971) patterned after that described by van Zinderen Bakker (1974). Carbon dioxide uptake or efflux was measured differentially with either a Beckman model 215 infra red gas analyzer (IRGA) spanned about 70 ppm full scale or with a UNOR II IRGA (Mahik, Hamburg) spanned 35 ppm full scale. The leaf was sealed into the cuvette around the petiole with Terostat VII (Terosan, Heidelberg). A flow chart of the analysis system and diagrams of the two cuvette types used are included in Appendix A.

Leaf temperature in the cuvette was controlled by either cooling the cuvette environment with a Peltier cooling unit (Borg Warner Thermoelectrics, model 920) switched on and off by a modified temperature sensing circuit (Ashe, 1972), by adjusting the temperature of the entire growth chamber, or by a combination of these methods , depending on which cuvette was being used. The temperatures of the air and leaf in the cuvette, and of the air and a comparable leaf outside the cuvette, were continuously monitored with .005 inch (5 mil) copper-constantan thermocouples (Omega engineering, Stamford, Conn.) pressed to their abaxial surfaces (Appendix A). In addition, soil temperature and clump temperature were monitored with 20 guage copper-constantan thermocouples insulated from moisture with a thin coating of epoxy. The IRGA and thermocouple outputs were continuously recorded with a Honeywell 24-channel multipoint strip-chart recorder equipped with an electronic reference junction for the thermocouples.

Figure 1. A single, attached *Dryas* leaf enclosed in the cuvette for measuring net assimilation and respiration rates.

Illumination was provided with the standard growth chamber lighting fixtures (p. 2), supplemented with either a mercury vapour lamp (400 watt, type 1220, Canadian General Electric Co., Ltd.), or a 1000 watt quartz-iodide lamp (Environmental Growth Chambers, Chagrin Falls, Ohio) suspended above the plant. The distance between the light source and the cuvette was varied to achieve different light intensities. Photosynthetically active radiation (PAR: 400 to 700 nm) was measured with a quantum sensor in microeinsteins per square meter per second ($\mu E\ m^{-2} sec^{-1}$) and illuminance was measured with a photometer in lux, both supplied by Lambda Instruments (Lincoln, Nebraska) with meter no. LI-185. Spectral analyses (ISCO spectroradiometer, Instrument Specialties Co., Lincoln, Nebraska) of these lamps are listed in Appendix B. The effects of both temperature and light on net assimilation were studied as outlined in Table 2. The plants were watered 6 to 12 hours before the start of each experiment.

The Effect of Temperature and Leaf Age on Gas Exchange.

In examining the direct effect of temperature on net assimilation of carbon dioxide, a leaf was subjected to a range of temperatures in approximately 5°C steps for 3 to 4 hours each, working from warm to cold. Dark respiration was monitored for one hour at the end of each temperature step. The influence of leaf age on net assimilation response to temperature was examined by starting one such experiment with an entire sprig of four leaves inserted into the cuvette. Response to the full range of temperatures was examined four times with the removal of the oldest remaining leaf after each series. The effect

Table 2. General experimental conditions for measuring the response of net assimilation rate to leaf temperature and light intensity.

Type of experiment	Light	Dark	Leaf temperature	Hours at each condition	Air flow rate ml min^{-1}	Order of changing conditions	Time for 1 experiment
Direct temp response	Constant	1 hr at end of each temp	Varied in 5° steps	3½ hrs	50-100	Warm to cold	1 to 1½ days
After effect of cold	"	"	"	"	"	Warm to cold, back to warm	3 days
Light response	Varied	2 hrs at start or end of expt	Constant	2 to 2½ hrs	"	High light to dark	1 day
Light response at various leaf temps	"	"	Varied at each light intensity (30°, 10°, 0°)	"	"	High light to dark, high temp to low	3 days

The plants were watered 6 to 12 hours before the start of each experiment.

of wound respiration from the cut ends of the petioles was eliminated from the cuvette environment by covering them with Terostat.

The After-Effect of Cold Treatment on Gas Exchange

The indirect or after-effect of cold temperatures on net assimilation was also examined. Net assimilation response was measured for a range of temperatures working from warm to cold with the coldest temperature several degrees below freezing (0°C) for 3 to 4 hours. Then the response was measured as the temperature was raised, stepwise, back to the initial (warmest) temperature. Again, dark respiration was measured for 1 hour at the end of each temperature step. In all cases, light intensity was constant.

The Effect of Light Intensity on Net Assimilation Rate

The response of net assimilation to light energy was examined by maintaining the leaf at a constant temperature and changing the incoming radiation every 2 to 3 hours following a change from light to dark. The light response was also examined at several leaf temperatures. In the latter case, light was held constant while the temperatures in question were attained in a stepwise manner, then the light intensity was decreased and again the response to the various temperatures was examined.

Photorespiration

Photorespiration was measured by examining the rate of net assimilation of CO_2 from bottled air (Linde, Consumers Welding, Edmonton) with about 2% O_2 and subtracting from this, the rate observed in 21% O_2 air.

Calculations for Gas Exchange Data

Calculation of Net Assimilation Rates

Each experiment lasted one to three days. At the end of an experiment, the leaf was harvested to determine its fresh and dry weight. The small size of the leaves (0.2 to 0.3 cm^2) made accurate measurement of leaf area impracticable. Net assimilation rates were therefore calculated on the basis of milligrams CO_2 assimilated per gram dry weight per hour (mg g^{-1} hr^{-1}) according to the following equation:

Net assimilation of CO_2 (mg g^{-1} hr^{-1}) =

$$\left(C \text{ ppm} \times Y \frac{\text{mg}}{\text{ml ppm}} \times \frac{273°K}{T_1 °K} \times F \frac{\text{ml}}{\text{min}} \times 60 \frac{\text{min}}{\text{hr}}\right) \div W_1 \text{ g} \qquad (1)$$

where: C = amount of CO_2 assimilated in ppm

Y = conversion from ppm to mg ml^{-1}

$$= \frac{44 \times 10^{-6}}{22.414} \text{ mg ml}^{-1}\text{ppm}^{-1}$$

T_1 = leaf temperature in °K

F = flow rate of air through the cuvette in ml min^{-1}

W_1 = dry weight of the leaf in grams

A negative value denotes net uptake and a positive value, net evolution of CO_2.

The system was set up to compare the cuvette air stream to the reference (ambient) air stream for 15 minutes and then to give a zero reference line by comparing two ambient air streams for 15 minutes. The data were therefore taken off the chart at half-hourly intervals, visually averaging over the 15 minute measuring period. The values thus obtained were then averaged over the 2 to 3 hour period at each set of conditions.

Calculation for the Response of Net Assimilation to Light

Because it was impossible to achieve exactly the same intensity of irradiance on the study leaves in repeated experiments, the individual data points for all measurements of net assimilation rate response to varying irradiance were scattered in 50 $\mu E\ m^{-2}sec^{-1}$ ranges around each attempted light intensity. Since a 50 $\mu E\ m^{-2}sec^{-1}$ (PAR) range is equivalent to only about one fortieth the intensity of full sunlight (1800 to 2000 $\mu E\ m^{-2}sec^{-1}$ PAR), these groups of data points were treated as units. The net assimilation rate means of these units were plotted against the means of the light intensities. Light response curves were fitted to the data with the following equation derived by Whitfield (pers comm) for the *Dryas* process model:

$$P_n = \frac{a \cdot L - R}{b \cdot L + 1} \qquad (2)$$

where: P_n = net assimilation rate

L = light intensity necessary to effect this rate

R = rate of respiration in the dark (at $L = 0$)

a,b= are arbitrarily chosen to fit the data

The magnitude of the net assimilation rate in response to increasing irradiance approaches an assymptote, called the light saturation point. The point at which net assimilation, for all practical purposes, reaches light saturation is therefore not clearly defined and has, in the past, been arbitrarily chosen by the experimenter in each study. This has led to difficulties in comparing the information presented by different authors. Therefore, in this study, the values of the light intensity required to bring about a rate of net assimilation equal to one half of the projected maximum rate at each temperature have been calculated to characterize these responses. However, it was still necessary to compare the data with light saturation values reported in the literature. Light saturation was therefore defined as that light intensity at which a 100% increase in irradiance would yield no more than a 10% increase in the net assimilation rate predicted by the equation (2) presented above.

Water Relations Experimental Methods

Equipment and General Methods

Psychrometers

Measurements of total water potentials (Ψ) and component water potentials (Ψ_p and $\Psi_{\pi+\tau}$, equation 3, p. 12) were made with Spanner-type psychrometers (C-51 psychrometer and HR33 Dewpoint microvoltmeter) supplied by Wescor Inc. (Logan, Utah) or constructed in the laboratory after Mayo (1974). In the latter case, samples were equilibrated in a

constant temperature water bath (32°C) and output was measured with a Fluke model 845 AB high impedance microvoltmeter. The chamber was 4 mm in diameter by 4 mm deep. Each sample consisted of one leaf cut in half to fit into the chamber. When the leaves were very dry or very small, two leaves were used per sample to ensure enough material to obtain an accurate measure of water potential. After the total water potential had been measured, the chambers plus samples were tightly wrapped in aluminium foil and placed in liquid nitrogen (-196°C) for 10 minutes to rupture the cell membranes, thereby eliminating the turgor pressure component. The samples were thawed at room temperature (10 minutes) and replaced in the psychrometers for measurement of the combined osmotic and matric components. An estimate of the original turgor pressure was calculated from the equation:

$$\Psi_p = \Psi - \Psi_{\pi+\tau} \quad (3)$$

where: Ψ_p = turgor pressure

Ψ = total water potential

$\Psi_{\pi+\tau}$ = combined osmotic and matric potentials

Potometers

Potometers were used to measure the rate of transpiration through excised shoots of *Dryas* and therefore , to estimate the leaf resistance to water loss. Due to the shortage of material and the necessity to conserve as much as possible, the plants could not be

submerged to cut the shoots under water. Water was placed on and around the portion of the stem to be cut in an attempt to avoid cavitation of the xylem sap when the cut was made. The excised shoots were immediately placed in water and the bottom section of each stem was cut off under water. The stems were threaded through stoppers and sealed in place with five-minute epoxy. Senescing leaves were removed and the remaining cut ends of their petioles were sealed with epoxy. The shoot-stopper complexes were inserted into potometers equipped with 0.2 ml pipettes to enable a fine measurement of water loss (Fig. 2). The open ends of the pipettes were covered with foil to prevent evaporation.

Experiments

Water Potentials Related to Phenology, Humidity and Net Assimilation

Water potentials of *Dryas* leaves were measured throughout the entire period of experimentation to establish the range found in laboratory-grown plants. In addition, several formal experiments were conducted with the sequential measurement of water potentials over time, in order to follow the pattern of change as the plants came out of or went into dormancy, and as they dried out during the summer season.

The effect of watering and of high humidity around the leaves was also examined by irrigating a plant thoroughly, placing a plastic bag over it (removed periodically to replenish CO_2), and following the leaf water potential over several weeks. An attempt was made to follow the influence of water potential on the rate of net assimilation of CO_2 by

Figure 2. A *Dryas* shoot set up in a potometer to measure the transpiration rate. This was then used to calculate leaf resistance.

enclosing a leaf in a cuvette for a three-week period. The plant was watered at the start of the experiment and then allowed to dry out. The rate of net assimilation of the leaf in the cuvette was measured periodically, always at the same time of day, and water potential was followed by sampling other leaves on the plant.

Water Potential Related to Leaf Resistance and Water Content

The leaf resistance of *Dryas* was measured over a three-week period during the late "summer". The plants had begun to show signs of leaf reddening, indicating the onset of dormancy, before the experiments were completed. Four potometers were filled with distilled water or solutions of mannitol varying in concentration to achieve solution water potentials of 0 to -6 bars. This resulted in tissue water potentials ranging from -8.5 to -48.2 bars. The experiments were conducted in a controlled environment growth chamber at 15°C air temperature (15.5°C leaf temperature), 200 to 250 $\mu E\ m^{-2}sec^{-1}$ PAR irradiance ($\simeq$ 10,000 lux), and 42 to 47% relative humidity with a wind speed of 1 to 3 mph past the leaves. The shoot-potometer system was allowed to equilibrate for one hour in this environment before the first reading was made. The amount of water lost was recorded at half-hourly intervals for 5 to 8 hours in the light, and overnight (8 hours) in the dark. The results showed no apparent rhythms so water loss rate was calculated over the whole light or dark periods. After the dark period, the lights were left on for 2 hours to ensure a return to steady state conditions in the light before the leaves were removed from the tops of their petioles, weighed, dried, and reweighed.

Samples of the leaves from each potometer were placed in psychrometers to measure total and component water potentials immediately after their fresh weight was determined. These samples were subsequently dried and the values of their fresh and dry weights were added to those obtained from the remaining leaves of each shoot. When all of the leaves had been removed, drops of five-minute epoxy were placed on the cut ends of the petioles. The amount of water lost from this system was again recorded for at least 3 hours. The rate of water loss from the potometer-shoot system minus leaves was thus measured and subtracted from the rate measured with the leaves. In this way, the calculation of transpiration rates could be restricted to that of mature, fully expanded leaves, by leaving the petioles and immature leaves intact in the potometers while the correction factor was being measured. Leaf resistance in the light and in the dark was calculated in the following way:

Leaf resistance (sec cm^{-1}) =

$$(A\ cm^2 \times (c_l - c_a)\ \frac{mg}{cm^3}) : F\ \frac{mg}{sec} \qquad (4)$$

where: A = leaf area in cm^2, one surface only since *Dryas* is hypostomatous

F = rate of water loss from the leaves in mg sec^{-1}

$(c_l - c_a)$ = difference in density of water vapour between the intercellular leaf spaces and the air in mg cm^{-3}, at their respective temperatures (Slatyer, 1967)

$$(c_l - c_a) = 0.289 \times \left(\frac{e_l}{T_l} - \frac{e_a}{T_a} \right)$$

e_l = vapour pressure of H_2O (mm Hg) in the leaf, assumed to be saturated

e_a = vapour pressure of H_2O (mm Hg) in the air

$$= \frac{\text{(relative humidity x saturated vapour pressure)}}{100}$$

T_l = temperature of the leaf in °K

T_a = temperature of the air in °K

The fresh and dry weight values of the leaves were used to calculate tissue water content as a percentage of the fresh weight. It was felt that the leaves did not reach full turgidity when distilled water was used in these experiments. Therefore, relative water contents were not calculated.

THE EFFECT OF TEMPERATURE ON NET ASSIMILATION

Literature Review

Leaf temperature is one of the main regulators of photosynthetic rates under natural conditions (Bosian, 1968). This is especially true in arctic and north temperate latitudes. Warren Wilson (1966) proposed that the growth of arctic plants was, in effect, temperature limited through a strong decrease in respiration at low temperatures causing a feedback inhibition of photosynthesis by accumulating sugars not respired away quickly enough. Miller and Tieszen (1972) in their arctic production model showed that air temperatures (which in many cases will be reflected in leaf temperatures) appear to be the principal factor involved in limiting plant production in the Point Barrow area. Billings and Mooney (1968) concluded that low temperatures and the long duration of snow cover were the main limiting factors of production by arctic and alpine plants. The response of net assimilation of mature *Dryas* leaves to temperature was examined to establish the upper and lower temperature limits of compensating gas exchange, the optimum temperature for net assimilation , and the rate of increase of dark respiration with temperature both before and after exposure to subfreezing temperatures. The effect of approaching dormancy and of leaf age on this response was also examined.

Direct Temperature Effect

The effects of temperature on photosynthesis have been widely studied in the past 20 years, giving rise to a number of theories as to the mechanisms involved in bringing about the observed responses. This work has been thoroughly reviewed by Bauer, Larcher and Walker (1974), in a series of papers by Pisek,Larcher and Unterholzner (1967; 1968b) and Pisek, Larcher, Moser and Pack (1969), and to a lesser extent by Larcher (1969) and Semikhatova (1960). The temperature effects on net assimilation can be divided into two categories: the direct effect and the after-effect. The latter can be further subdivided into photosynthetic acclimation to the prevailing temperature conditions and damaging of the photosynthetic apparatus by exposure to extreme temperatures.

The immediate response of net assimilation to leaf temperature changes follows an optimum curve as that described in a model by Hesketh and Baker (1967). The shape of this curve and its position on the temperature scale will vary with species. Other factors such as light intensity, temperature history and phenology also have a role in determining the shape of the temperature response of net assimilation. These will be discussed later.

The temperature responses of net assimilation by various species as presented by Murata and Iyama (1963), Hofstra and Hesketh (1969) and Pisek and Winkler (1959) suggest that the direct response of net assimilation by C_3 plants is relatively insensitive to temperature

changes , that is, they respond optimally or near-optimally over a broad range (10° to 25°C) of temperatures. Zelitch (1971) has proposed that this may be due to rapid increases of photorespiration with temperature paralleling increases in photosynthesis up to the photosynthetic temperature optimum. This would have a net effect of creating a broad plateau of maximum net assimilation rates. Similar responses for the C_4 plants studied by Murata and Iyama (1963) and by Hofstra and Hesketh (1969) show a much more pronounced temperature effect with a narrow optimum range.

Pisek and Winkler (1959) pointed out that the temperature response of net assimilation of conifers was not symmetrical about the optimum, but decreased rapidly at high temperatures. The assymetrical shape is again obvious in the responses supplied by Hofstra and Hesketh (1969) for all of the species they examined.

The temperature response of net assimilation can be defined by its upper and lower temperature limits for positive net assimilation, the optimum temperature for net assimilation, and the rate at this temperature. The optimum temperature for net assimilation by C_3 plants tends to be quite variable, ranging from 10° to 30°C depending on many other factors (Hofstra and Hesketh, 1969). C_4 plants tend always to have a high optimum temperature (Murata and Iyama, 1963; Hofstra and Hesketh, 1969). The optimum temperatures for net assimilation of arctic and alpine species range from 10° to 25°C (Table 3). The upper and lower temperature limits for compensating net assimilation also vary with species and conditions. The lower temperature limit for positive net assimilation of chilling sensitive plants may be in the vicinity of 0° to 5°C (Ludlow and Wilson, 1971) while frost hardy plants,

Table 3. Optimum temperatures for net assimilation of various arctic and alpine plants.

Species	Temperature °C	Reference
Oxytropis	7°	Gerasimenko and Zalensky , 1973
Primula	12°	" "
Caltha	13°	" "
Dryas integrifolia	9°- 14°	this study
Oxyria digyna	10°- 15°	Pisek *et al.*,1969
Ranunculus glacialis	13°- 21°	" "
Geum reptans	16°- 21°	" "
Artemesia	20°	Gerasimenko and Zalensky , 1973
Antennaria	20°	Mooney, Wright and Strain, 1964
Eriogonum	20°	" "
Erigeron	20°	"
Hymenoxys	20°	"
Thalictrum alpinum	20°- 25°	Mooney and Johnson, 1965
Oxyria digyna	25°	Mooney and Billings, 1961

especially those which achieve their hardiness by freezing avoidance, may assimilate CO_2 positively at temperatures as low as -5°C (Pisek *et al.*, 1967). In the latter case, the lowest temperature for positive net assimilation tends to coincide with the freezing point of the tissue (Pisek *et al.*,1967; Larcher, 1969). The upper temperature compensation point is not as sharply defined as the lower limit for each individual plant. It can be altered by acclimation (Bauer, 1972). Since respiration, photorespiration and thermal denaturation of proteins are the main causes of the decline of net assimilation at high temperatures (Bauer *et al.*,1974), the rate of increase of respiration and the species' sensitivity to thermal protein denaturation will determine the upper temperature limit of positive net assimilation. This boundary is usually in the 35° to 45°C range. The upper limit for compensating net assimilation by arctic and alpine shrubs is between 40° and 44°C (Pisek and Kemnitzer, 1968).

After-Effects of Extreme Temperature

In addition to the direct effects of temperature on the rates of photosynthesis and respiration, the temperature-related net assimilation pattern is made more complex by after-effects of cold or warm temperatures of various durations, intensities and repetitions. It has been found that many species acclimate photosynthetically to the temperatures at which they are grown. That is, their gas exchange capacity alters, usually in the direction of greater efficiency at the temperature to which they were conditioned (Mooney and Shropshire, 1967), thereby causing a shift in the temperature optimum. This effect has

been demonstrated with a wide range of plant types including grasses (Charles-Edwards, Charles-Edwards and Cooper, 1971), cotton (Downton and Slatyer, 1972), conifers (Rook, 1969), and arctic and alpine species (Billings *et al.*,1971; Smith and Hadley, 1974; Mooney and Johnson, 1965). It appears then, that the acclimation response is widespread. There are differences in the extent of photosynthetic acclimation and in the length of exposure required to bring about this readjustment. Some plants do not readily acclimate to different environments. Treharne and Eagles (1970) found no significant interaction of growth temperature *versus* analysis temperature for *Dactylis glomerata*.

Mooney and Harrison (1970) have speculated on the mechanism involved in bringing about acclimation of net assimilation to temperature. They found with *Encelia californica*, that accompanying adjustment to warm temperatures, there was a reduction of the mesophyll resistance to CO_2 transfer, a decrease in the oxygen inhibition of photosynthesis (photorespiration) and a decrease in stomatal resistance to H_2O and CO_2 transfer. It was suggested that these phenomena might be interrelated. The acclimation has been shown to occur within 24 hours (Mooney and Shropshire, 1967). Pharis, Hellmers and Schuurmans (1967) found that acclimation to warm temperatures was more rapid than to cold temperatures.

In addition to the conditioning of net photosynthetic response to the prevailing temperature regime, there are after-effects on net photosynthesis caused by stressing temperatures which may be damaging

the mechanism in some way. There is some evidence of acclimation in this respect as well, in that the same stressing temperature applied repeatedly may not result in as much damage at subsequent applications, after full recovery, as at the first. This relates to heat and frost hardening. Pharis, Hellmers and Schuurmans (1970) found that exposure of conifers to subfreezing nights (-2°C) would depress the rate of net assimilation at warmer temperatures the following day, and that the recovery time from this effect was longer than 20 days. Exposure to subzero temperatures above the freezing point of the leaves had no effect on subsequent net assimilation rates of *Abies alba* in the autumn (Pisek and Kemnitzer, 1968a) or of *Leucoium vernum* (Pisek *et al.*,1967). At the point of leaf freezing (-4° to -6°C), injury occurred, accompanied by a marked decrease in net assimilation rate at higher temperatures. They found that if the leaves were not injured at this temperature, there was no after-effect on net assimilation rates. This is contradicted by observations of a depression of net assimilation rate and an increase in the respiration rate of *Abies alba* after exposure to non-injurious cold temperatures (Bauer, Huter and Larcher, 1969). The reduction in the net assimilation rate of apparently uninjured leaves may be explained by a negative effect on the rate and extent of stomatal opening following exposure to cold (5°C) as observed with sorghum (Pasternak and Wilson, 1972). Delay in growth of temperate and subtropical grasses after exposure to 0°C has been related to ultrastructural changes in their chloroplasts (Kimball and Salisbury, 1973).

Very warm temperatures have also been found to induce an after-effect on net assimilation at lower temperatures (Lyutova, 1962; Bauer, 1972). The net assimilation rate of *Abies alba* and *Acer pseudoplatanus* recovered with time if there were no necrotic injuries, at a rate dependent on the degree of heat to which they had been exposed. Both Lyutova and Bauer found that the heat resistance of photosynthesis had increased with subsequent exposure to high temperatures.

Results and Discussion

Direct Effect of Leaf Temperature on Net Assimilation

The direct response of net assimilation of CO_2 to temperature by individual leaves of *Dryas integrifolia* from Devon Island is presented in Fig. 3. For plants in the actively growing state, this response is characterized by a minimum leaf temperature limit of -5° to -6°C, a maximum limit near 40°C and an optimum temperature range between 9° and 14°C. The mean maximum rate of net assimilation for eight individual leaves within this optimum range was 18.7 mg g^{-1} hr^{-1} at light intensities greater than 400 μE $m^{2}sec^{-1}$(PAR). The lower temperature limit coincides with the freezing point observed for needles of north-temperate conifers (Pisek *et al.*,1967). The fact that the freezing point of the leaves is below 0°C, suggests that *Dryas*, at least in its summer state, makes use of an avoidance mechanism of frost hardiness (Levitt, 1972). The upper temperature limit for positive net

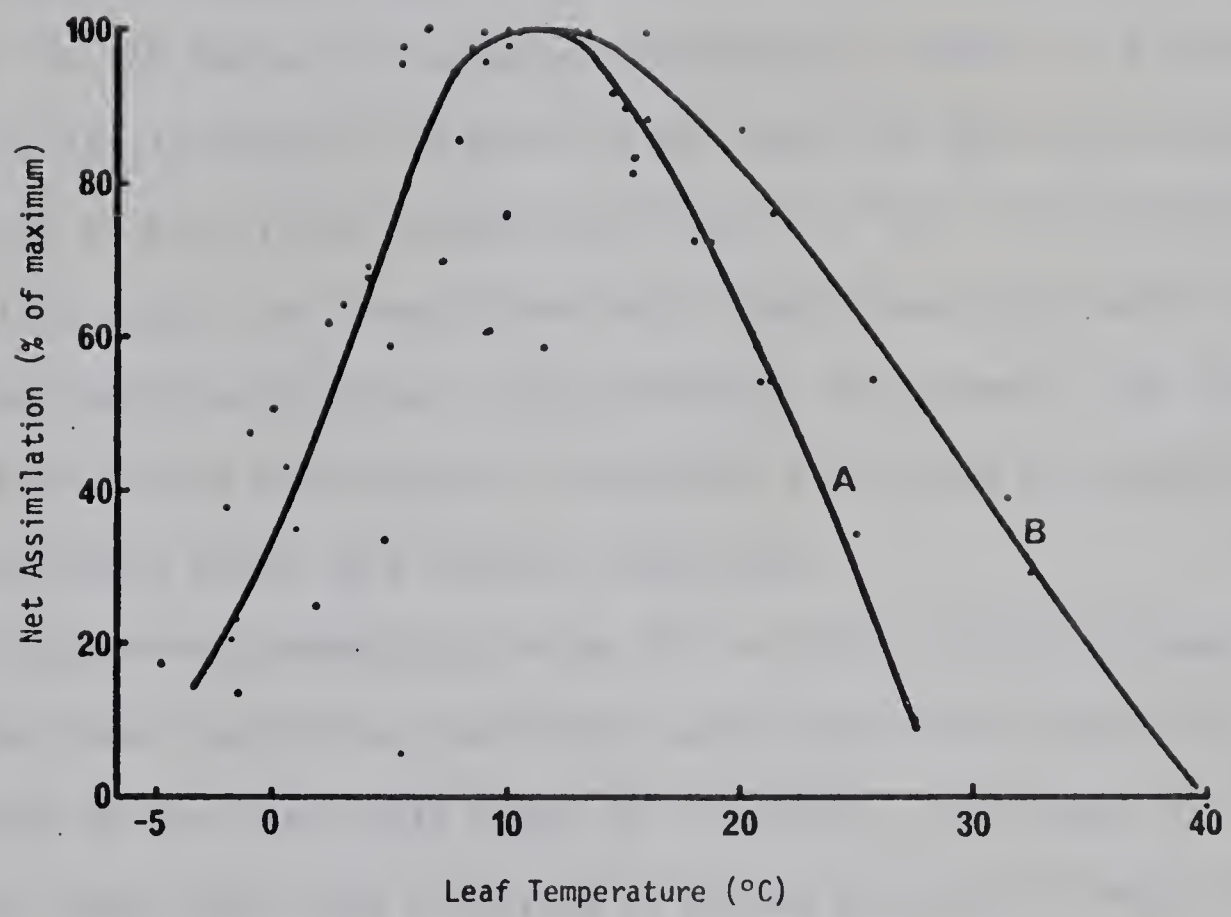


Figure 3. The effect of leaf temperature upon net assimilation by *Dryas integrifolia*; plotted as a percentage of the maximum rate for each experiment. The data presented are for 7 experiments. A : Irradiance = 250 to 300 μE $m^{-2}sec^{1}$; B : Irradiance = 900 to 1000 μE $m^{2}sec^{1}$ (PAR).

assimilation falls into the range (40° to 44°C) exhibited by arctic shrubs (Pisek *et al.*,1968b). Since *Dryas* leaf temperature is uncoupled from air temperature (Mayo *et al.*,1973; Biebl, 1968), sometimes rising to above 35°C, this upper compensation point may be as important as the lower limit in determining the net assimilation balance of *Dryas* in the field. In the course of measuring temperature-related net assimilation rates in the laboratory, it became clear that the upper limit reached 40°C only at high light intensities (1000 μE m ^{2}sec^{-1} or 60,000 lux). Since high *Dryas* leaf temperatures were always associated with high incoming radiation on Devon Island (Addison, pers. comm.), the leaves should still have the capacity to maintain a positive net assimilation balance except under very extreme conditions.

The optimum temperature range (9° to 14°C) for *Dryas* leaves examined under controlled conditions agrees well with that (10°C) indicated by the field data (Mayo *et al.*,1973). This range is somewhat lower than that exhibited by alpine and arctic shrubs (15° to 20°C, Table 3, p. 21). There was no noticeable shift in the optimum between plants raised in a constant 10°C temperature regime and those raised in the fluctuating (0°C to 10° and 30°C) regime. This suggests that *Dryas integrifolia* does not readily acclimate photosynthetically to different temperature regimes.

The maximum rate of net assimilation (18.7 mg g^{-1} hr^{-1} or roughly 21 mg dm^{-2}hr^{-1} counting one surface only) falls into the lower end of the range of rates commonly exhibited by temperate C_3 plants (El-Sharkaway and Hesketh, 1965). It is somewhat lower than rates

measured for alpine herbs (22 to 30 mg g^{-1} hr^{-1}, Pisek *et al.*,1969) and higher than that measured for trees (2 to 9 mg g^{-1} hr^{-1}, Larcher, 1969). The comparison is, however, somewhat invalidated by the inclusion of non-photosynthetic tissues in determining these rates. The maximum rate of net assimilation measured for entire plants of *Dryas integrifolia* under natural conditions on Devon Island was 7.4 mg g^{-1} hr^{-1} (Thompson *et al.*,1973). The maximum published rate measured for *Dryas punctata* in Western Taimyr (Shvetsova and Vosnesenski, 1971) was 9.5 mg g^{-1} hr^{-1}. There is therefore, a two-fold difference between the individual leaf rate and the entire plant rate of net assimilation. This can be explained in several ways. The net assimilation studies in the field were conducted on whole plants including all of the non-photosynthetic tissues whose respiration activity would decrease the possible observed net assimilation rate. In the natural situation, all the leaves in a clump of *Dryas* are not experiencing the same temperature and light conditions so that they could not all be assimilating under optimum conditions at one time. The different age-classes of leaves will also be assimilating CO_2 at different rates (Fig. 10, p. 49). Leaf water potentials in the field were generally lower than those of laboratory grown plants (-11 to -53 bars as compared with -10 to -30 bars respectively, p. 63). These factors would all contribute to reduce the maximum observable rate of net assimilation in the field. It should also be noted that as the tissue temperature rises, its rate of respiration will increase, possibly at a rate similar to that measured for the leaves (Fig. 7a, p. 41). This would cause the rate of

net assimilation of the entire plant to decrease much more rapidly with temperature than is depicted in Fig. 3 (p. 26) for individual leaves. The maximum temperature limit for positive net assimilation would therefore be somewhat less for whole plants than that measured for individual leaves.

The shape of the temperature response curve for *Dryas* leaves differs from the characteristic response (literature review, p. 20) in that it does not decrease so rapidly at higher temperatures (Fig. 3, p. 26). This is due to the wider span between the temperature for optimum net assimilation and the upper limit for positive net assimilation than normal because of the unusually low optimum temperature exhibited by the net assimilation of *Dryas*.

Effect of Approaching Dormancy on Net Assimilation

There is a marked decrease in net assimilation rate with the onset of dormancy at the end of the summer season. Fig. 4 shows the absolute response of net assimilation to temperature by a leaf which was going dormant, plotted below that of leaves in the fully active state. The maximum rate of net assimilation of the former was 3 mg g^{-1} hr^{-1} as compared with 18.7 mg g^{-1} hr^{-1} for the non-dormant leaves. Although there is a considerable downward shift in the upper temperature limit for positive net assimilation, the optimum temperature remains the same, though the response is of necessity more flattened. This decrease in net assimilation rate is accompanied by a decrease in the rate of dark respiration (Fig. 7a, p. 41), indicating that the actual capacity for

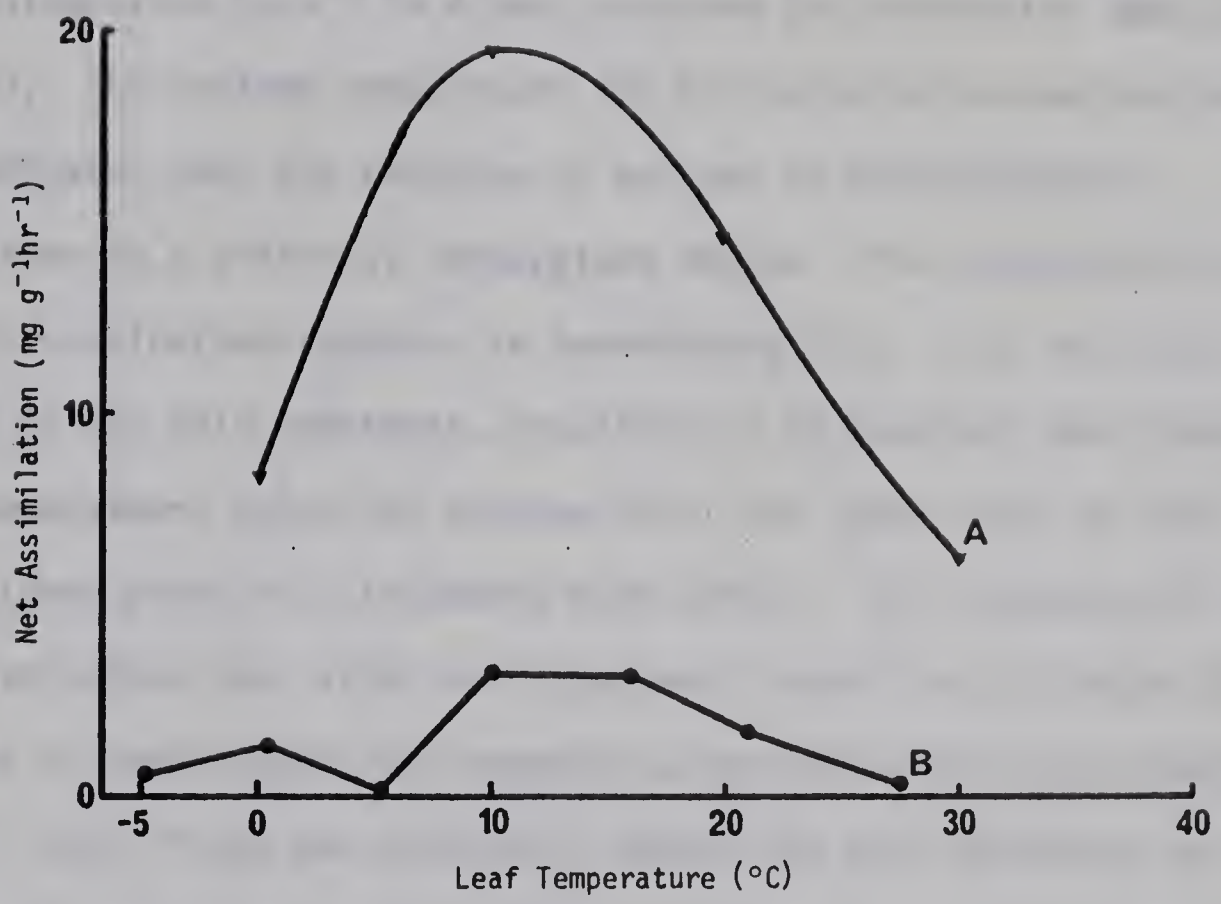


Figure 4. The effect of approaching dormancy of *Dryas integrifolia* on the response of net assimilation by an individual mature leaf to temperature. A : Plants in the active state. The values were interpolated from the data presented in Fig. 11 (p. 57) at 810 µE $m^{2}sec^{-1}$ (PAR). B : Plant approaching dormancy, well watered. Irradiance was 810 µE $m^{-2}sec^{-1}$.

gross photosynthesis had decreased. The reduction in net assimilation rate may be due to a loss of or masking of chlorophyll.

After-Effect of Low Temperature on Net Assimilation

Net assimilation of *Dryas* leaves at 10°C was reduced to 65% of its previous rate by a 3 to 4 hour exposure to subfreezing temperatures (Fig. 5). The optimum temperature for net assimilation was not affected. This indicates that the response is not one of photosynthetic acclimation to a different temperature regime. The characteristics of the dark respiration response to temperature (Fig. 7, p. 41) were also changed by the cold treatment, resulting in no apparent rate changes at leaf temperatures below the optimum 10°C, but lower rates at high temperatures after cold treatment than before. The reduction of the net assimilation rate after cold treatment cannot be attributed to an increase in respiration rate commonly associated with tissue damage (Levitt, 1972; Pisek and Kemnitzer, 1968a) and must therefore be due to a change in the actual photosynthetic system or to an after-effect on stomatal opening as observed by Pasternak and Wilson (1972). Since the leaf under examination in each experiment was receiving more direct radiation than the rest of the plant, and since the main method of temperature control was by adjusting the whole growth chamber temperature, that portion of the plant not under investigation was of necessity subjected to temperatures below (about 5°C) those experienced by the experimental leaf. It is therefore possible that the decrease in net assimilation rate exhibited by this leaf was in part a reflection of a stress response by the rest of the plant. The increase of net

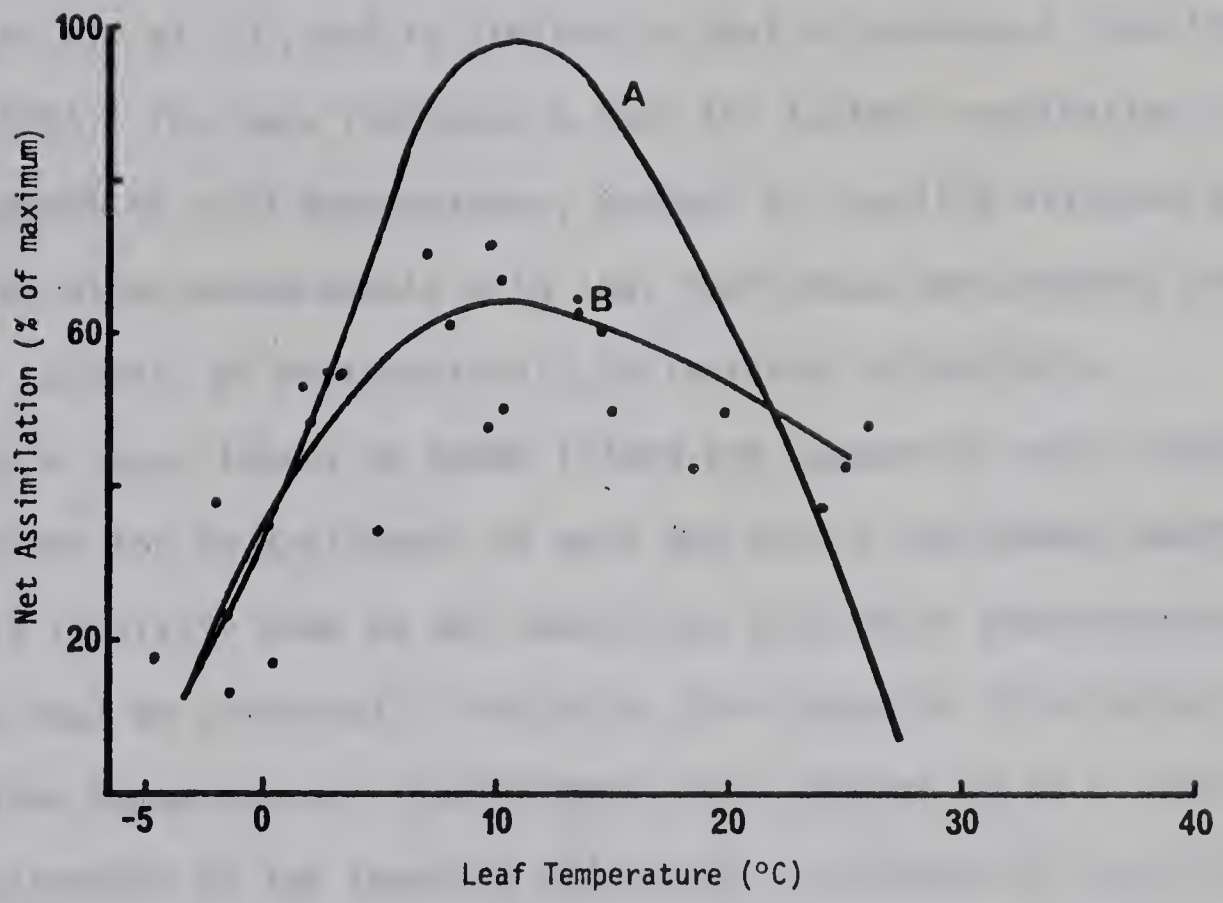


Figure 5. The effect of sub-zero leaf temperature on net assimilation by *Dryas integrifolia* at subsequent higher temperatures. Irradiance : 260 to 800 μE $m^{-2}sec^{-1}$ (PAR). The data are cumulative over 4 experiments. A : Before cold treatment (as presented in Fig. 3, p. 26) B : After cold treatment at -0.5° to -4.5°C leaf temperature for 3 to 4 hours. Data points are for B only.

assimilation at 10°C over a 20 hour period starting one day after a cold treatment (Fig. 6) suggests that recovery from the cold stress is slow . After 40 hours, net assimilation had recovered to 72% of its original rate from 43% of the original at 21 hours after the end of the cold treatment. This recovery is more rapid than that exhibited by Douglas fir at 3°C, and is similar to that of ponderosa pine (Pharis *et al.*,1970). The data indicates a need for further examination of this response to cold temperatures, perhaps by coupling attached leaf net assimilation measurements with leaf resistance measurements and with the capacity of photosynthesis by isolated chloroplasts.

Since *Dryas* leaves on Devon Island are exposed to near freezing temperatures for several hours of each day during the summer months, one would initially come to the conclusion that their photosynthetic capacity must be continually limited by this negative after-effect of subfreezing temperatures. Furthermore, this appears to be a ready-made explanation of the two-fold difference in maximum net assimilation rates observed between the field and laboratory studies (p. 28). However, the same before and after cold treatment responses were observed for leaves which had been grown under the constant 10°C temperature regime as for those which had been grown under a fluctuating regime which caused their leaf temperature to decrease to 0°C for several hours every day. Leaves treated in the latter manner still exhibited maximum rates of net assimilation as high as those of leaves grown at 10°C only. The photosynthetic apparatus of leaves which are subjected to daily temperatures of 0°C must therefore either adapt back to a higher capacity or it is not altered by exposure to these temper-

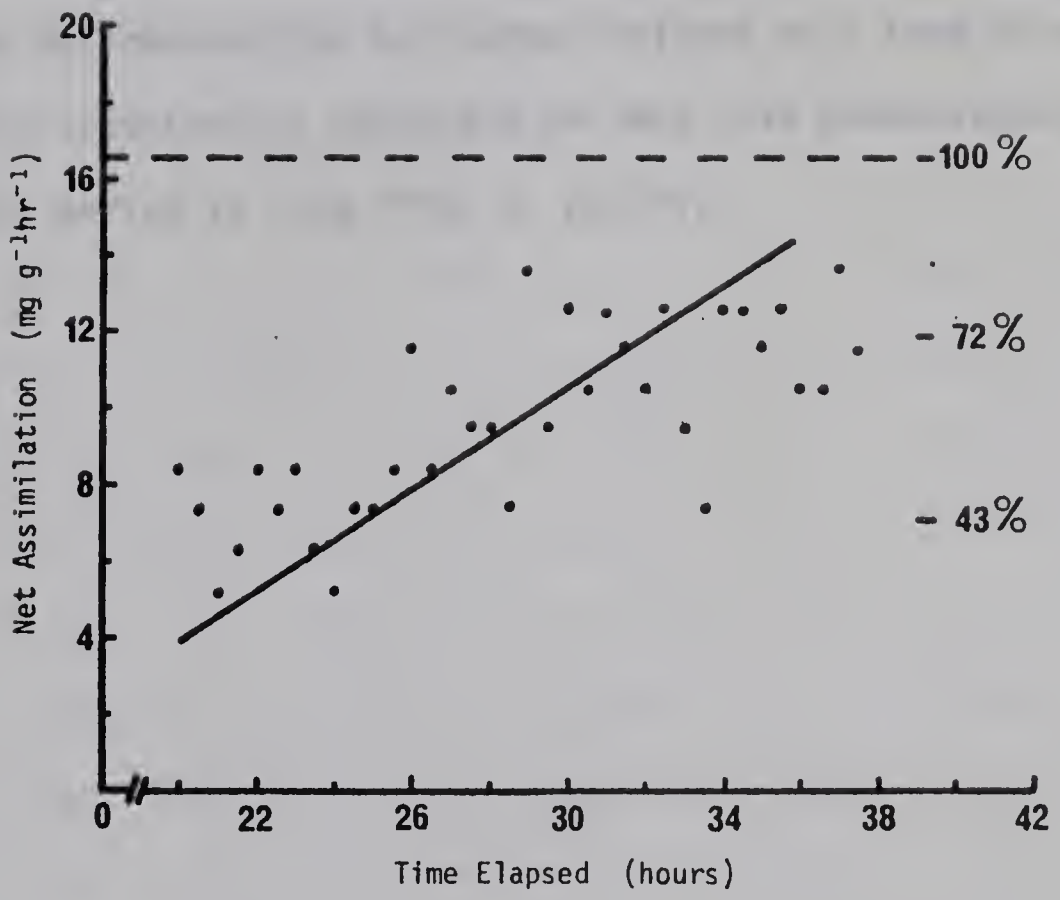


Figure 6. The recovery of net assimilation rates by *Dryas* leaves at 10°C after a 3 hour treatment at -2°C. Leaf temperature was raised stepwise back to 10°C during a 20 hour period, then left at 10°C. The rate at 10°C before the cold treatment is shown as 100%

atures. Since the leaves are receiving continuous radiation on Devon Island, they will not often experience temperatures much below 0°C and therefore this effect of exposure to subfreezing temperatures is probably not a major reason for the differences in net assimilation rates between the field and laboratory data. It might well play a role in determining the net carbon balance on a long term basis if the plant is occasionally subjected to very cold temperatures because the recovery period is long (Fig. 6, p. 34).

THE EFFECT OF TEMPERATURE ON RESPIRATION

Literature Review

Dark respiration increases exponentially with temperature (Larcher, 1969), and although it is one of the most heat stable life functions, there is a clear depression of carbon dioxide release by pea and wheat seedlings within a few hours of exposure to temperatures above 40°C (Bauer *et al.*,1974; Levitt, 1972). Forward (1960) found no evidence of acclimation of dark respiration to temperature within the non-injurious range in all of the literature she reviewed. This has been more recently supported by Mooney and Harrison (1970) with *Encelia*, but Billings *et al.* (1971) found that the rate of dark respiration of *Oxyria digyna* increased with acclimation to cold temperatures. Semikhatova (1962) found that exposure of several alpine species to -7°C caused a subsequent decrease in respiration at 20°C. There are, therefore, conflicting reports about the ability of dark respiration to acclimate to temperature, and it is likely that this is a species-related phenomenon and not necessarily universal.

The Q_{10} of dark respiration is normally 2 to 3 between 10° and 20°C leaf temperature and appears to be uniform for all plant groups regardless of the latitude of their origin (Forward, 1960). Larcher (1969) cites the Q_{10} of dark respiration of trees to be between 1.5 and 2.5 while Semikahatova and Shuktina (1973) present respiration data which have approximate Q_{10}'s of 1.9 to 3 for some arctic species.

There are indications that, although the Q_{10} of dark respiration is relatively uniform throughout the world, there are differences in respiration rates correlated with habitat. A trend of higher respiration rates in species living in cold environments over those living in temperate and tropical regions has been observed (Billings and Mooney, 1968). Forward (1960) has calculated that the respiration rate of tropical species at 30°C is equal to that of arctic species at 10°C. Pisek and Winkler (1958) found that *Picea excelsa* growing at high altitudes had higher respiration rates at equivalent temperatures than those growing in a valley. Mooney and Billings (1961) observed the same in northern versus southern populations of *Oxyria digyna* and suggest that the high respiration rates of plants in the north help them to develop more rapidly in the cold. These observations are contradicted by an investigation conducted by Scholander and Kanwischer (1959) in which they found no difference in the respiration rates between southern (Massachusetts) and northern (Labrador) populations of seven out of nine species tested (*Cladonia spp* , *Equisetum*, *Lycopodium*, *Arenaria*, *Epilobium*, and *Campanula*). The trend is further obscured by the observation that alpine deciduous shrubs have higher respiration rates than evergreen shrubs (Pisek and Knapp, 1959). This may be a reflection of a greater need to produce photosynthesizing material quickly (Hadley and Bliss, 1964). Cold-acclimated evergreen shrubs should therefore have dark respiration rates intermediate between those of temperate species and of cold-climate deciduous species. The available data do not completely support this idea (Table 4). It is clear that no definite conclusions can be drawn regarding a trend in rates of dark respiration

Table 4. Dark respiration rates of various species measured at 20°C.

Species	Rate mg $g^{-1}hr^{-1}$	Type	Reference
Chrysothamnus isidiflorus	10	deciduous	Mooney, Wright and Strain, 1964
Picea excelsa	8	evergreen	Pisek and Winkler, 1958
Dryas integrifolia	7.9	"	this study
Thalictrum alpinum	4.5-5.6	deciduous	Mooney and Johnson, 1965
Purshia glandulosa	3.3	evergreen	Mooney, Wright and Strain, 1964
Chamaebataria millefolium	3.18	"	" "
Artemesia spp (high altitude)	2.1-2.4	"	" "
Compositae	2.0-2.7	deciduous	" "
Deciduous trees	1.8 avg	"	Larcher, 1969
Ledum groenlandicum	1.0-1.5	evergreen	Smith and Hadley, 1974
Coniferous trees	0.65 avg	"	Larcher, 1969
Pinus spp	0.31-0.57	"	Mooney, Wright and Strain, 1964

for deciduous as compared with evergreen cold-climate species and that the observed tendency for respiration to increase with latitude is not all-inclusive, but does appear to exist for certain species.

It has been observed that the rate of dark respiration decreases as plants enter the dormant state. Pisek and Winkler (1958) observed a 5°C upward shift in the response of respiration of *Picea excelsa* to temperature in winter. Wager (1941) also observed a decrease in respiration rates in winter, but attributed this to leaf age effects and inclusion of stems in the sample rather than to an actual decrease in metabolic activity or ability. Zeller (1951) associated decreases in dark respiration rate with frost hardening in autumn.

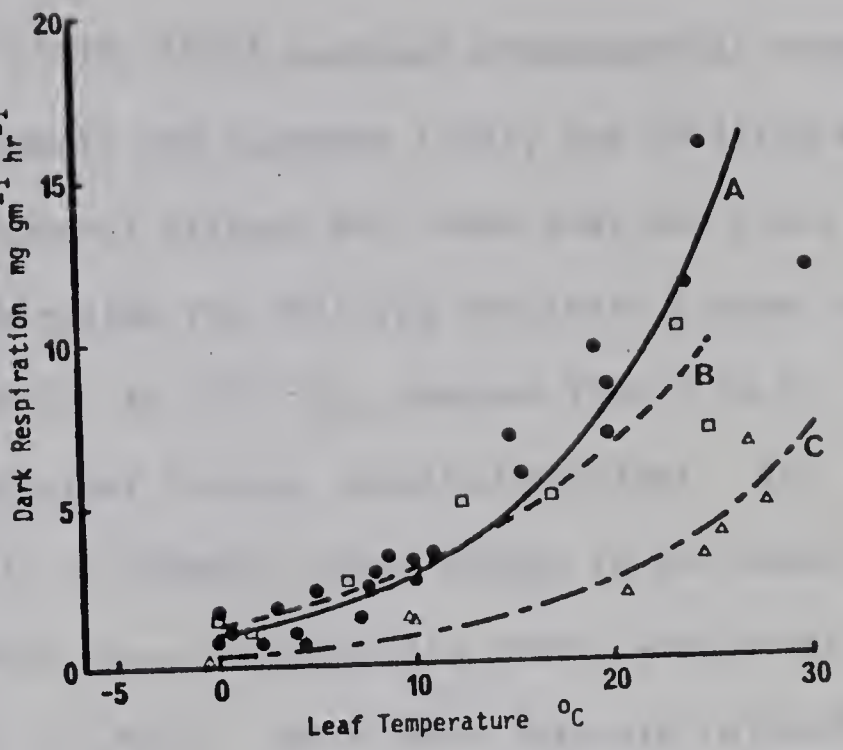
There are definite indications that the process of dark respiration is severely inhibited in leaves in the light (Hofstra and Hesketh, 1969; Mangat, Levin and Bidwell, 1974). This is possibly due to the abundance of ATP energy produced by photophosphorylation reactions causing a feedback inhibition of the dark respiration ATP-producing processes. Dark respiration responses cannot therefore be automatically related to net assimilation rates in the light to achieve a complete understanding of the carbon exchange balance of a leaf. This is especially true under conditions approaching the light saturation of photosynthesis. However, photorespiration, which is prevalent in C_3 plants (Bull, 1969; Black, 1973), is an important factor to be considered in conjunction with net assimilation rates in the light. Hofstra and Hesketh (1969) have found that photorespiration is generally 1.3 to 2 times greater than dark respiration at low leaf temperatures (15° to 40°C) but that above 40°C, dark respiration is

greater than photorespiration. Photorespiration tends to have an optimum temperature range near to that of photosynthesis (Hofstra and Hesketh, 1969), whereas dark respiration does not. These general observations on photorespiration are based on the responses of agricultural plants growing in temperate climates, and are not necessarily applicable to other situations.

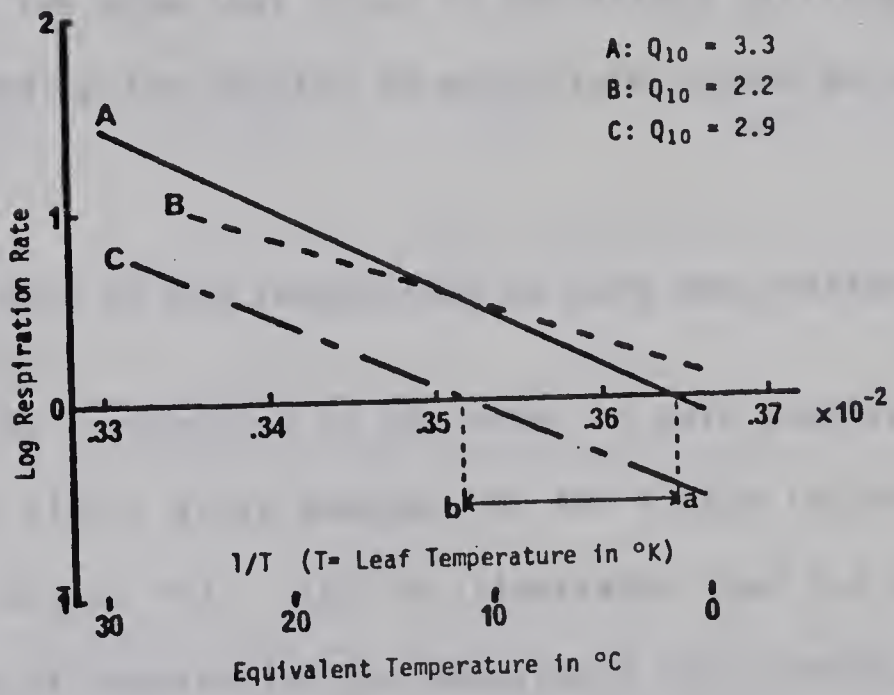
Results and Discussion

Direct Effect of Leaf Temperature on Dark Respiration

The rate of dark respiration of single mature leaves of *Dryas integrifolia* (Fig. 7a) is higher than most of the rates observed for other species (Table 4, p. 38). The actual values and their rate of increase with temperature are similar to those of summer respiration in *Picea excelsa* (Pisek and Winkler, 1958) and much higher than those of *Ledum groenlandicum* (Smith and Hadley, 1974, Table 4). *Dryas* dark respiration is equal to or greater than that of arctic and alpine deciduous species. This does not support the idea, discussed in the literature review (p. 37), that the rate of respiration by evergreens is less than that by arctic deciduous species. The high rate of respiration at low temperatures does support the theory that cold climate species have higher rates of respiration than temperate species. For *Dryas* , when this is combined with the low optimum temperature (10°C) of net assimilation (Fig. 3, p. 26), it is apparent that this species is well adapted for both metabolism and photosynthesis at the low temperatures found in its natural habitat.



a) Dark respiration rates as affected by temperature



b) Arrhenius plot of dark respiration

Figure 7. The effect of leaf temperature on the rates of dark respiration of single *Dryas* leaves in their actively growing state, before (A) and after (B) cold treatment (-.5°to -4.5°C), and when they are approaching dormancy (C). Low temperatures have the effect of noticeably changing the slope of the Arrhenius plot and Q_{10} (7b), although this is only apparent in respiration rate changes at temperatures above 15°C (7a). The approach of dormancy (C) causes a marked decrease in respiration rates as compared with those of non-dormant leaves at equivalent temperatures (7a). The pattern of response remains almost the same, but is shifted 10°C upward along the temperature axis from a to b (7b).

Lyons (1972; 1973) examined mitochondrial respiration of chilling sensitive (tomato and cucumber fruit) and chilling resistant (beet roots and potato tubers) tissues and found that the slope of the Arrhenius plot of respiration for chilling sensitive tissues was discontinuous in the range of 10° to 12°C (Q_{10} changed from 2 to 6), while that of chilling resistant tissues remained constant. Fig. 8 (p. 43) suggests that there is no dramatic phase change in the overall dark respiration of non-dormant *Dryas integrifolia* leaves within the temperature range examined (0° to 30°C). When these data are related to Lyons' results, they support the view that *Dryas* is definitely chilling resistant, as is also evidenced by its ability to assimilate carbon at temperatures to -5°C (p. 25).

After-Effect of Low Temperature on Dark Respiration

There is a reduction in the rates of dark respiration at high temperatures (15°C) after exposure of the tissue to subfreezing temperatures (Fig. 7a, p. 41). Fig. 7b illustrates that the whole pattern of the response of respiration to temperature has changed, with an alteration of the Q_{10} from 3.3 to 2.2 . The observed rate reduction is in contrast to the increased rates accompanying cold acclimation by net assimilation observed by Billings *et al.* (1971). It resembles the decrease in respiration after exposure to -7°C by alpine plants as recorded by Semikhatova (1962). A more detailed examination of this response would be necessary before valid conclusions could be drawn as to whether it is due to temperature acclimation in the real sense, or to some sort of short-term injury or mechanical inhibition.

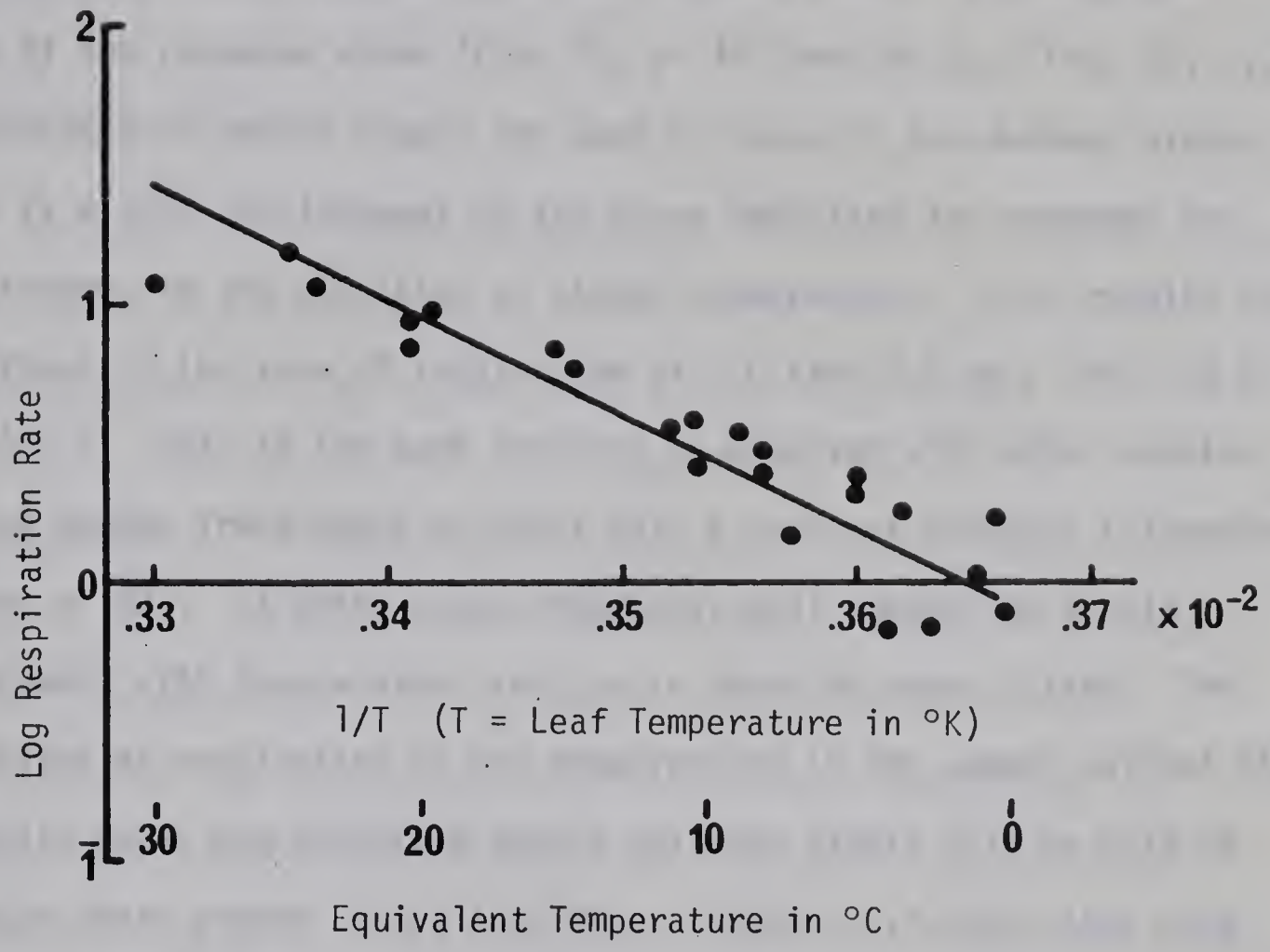


Figure 8. An Arrhenius plot of the dark respiration rate of single *Dryas* leaves showing that the data points fall along a straight line between 0°C and 30°C. This supports the view that *Dryas integrifolia* is chilling resistant. Chilling sensitive plants should show a noticeable inflection point around 10° to 12°C (Lyons, 1972).

The Effect of Dormancy on Dark Respiration

The dark respiration rates of *Dryas integrifolia* decrease significantly as the plants enter the dormant state. Although the shape of the response curve (Fig. 7a, p. 41) and the Q_{10} (Fig. 7b, Q_{10}= 2.9 versus 3.3) remain almost the same as those of non-dormant plants, there is a 10°C displacement of the curve depicting the response to temperature, in the direction of higher temperatures. This results in a decrease in the rate of respiration at 0°C from 1.0 mg $g^{-1}hr^{-1}$ to 0.3 mg $g^{-1}hr^{-1}$. This is the same response as observed with other species as they become frost-hardy or enter into a state of dormancy (literature review, p. 39). It makes *Dryas* remarkably well adapted to a cold environment with long winters such as is found on Devon Island. The high rates of respiration at low temperatures in the summer reflect high metabolic rates and therefore ensure that the plants will be able to maximize their growth during this time. However, if such rates were maintained during the autumn and winter, much of the plants' energy reserves could be respired away. Respiratory gas exchange has been measured at temperatures as low as -17°C for *Pinus sylvestris* (Ungerson and Scherdin, 1968) and -26°C for arctic lichens (Scholander *et al.*, 1953). This means that gas exchange under the cold winter conditions cannot be ignored as insignificant, especially as the winter dark period is long. It may therefore be very important to the survival of *Dryas* plants on Devon Island that the rate of dark respiration at a given temperature decreases with the onset of dormancy. This is especially

true in the autumn when the plants start experiencing longer and longer dark periods in a temperature range that might still result in considerable respiratory loss over a long period if the rates did not decrease.

Photorespiration

The increase in rate of photorespiration (Fig. 9) follows closely that of dark respiration in *Dryas* leaves up to 30°C, which is its optimum temperature. At higher temperatures it decreases. Hofstra and Hesketh (1969) found a similar trend in the response of photorespiration to temperature in sugarbeets, soybeans and *Atriplex hastata*. These results differ from the expected response in two ways: the rate of photorespiration is usually higher than that of dark respiration at low temperatures; and the optimum temperature for photorespiration usually coincides with that of net assimilation (literature review, p. 40). Photorespiration could scarcely be detected below 15°C and is therefore probably not a significant drain on the net carbon balance below this temperature. The equality between the rates of dark respiration and photorespiration up to 30°C is not necessarily due to a below normal rate of photorespiration but probably to the high rates of dark respiration measured for *Dryas*.

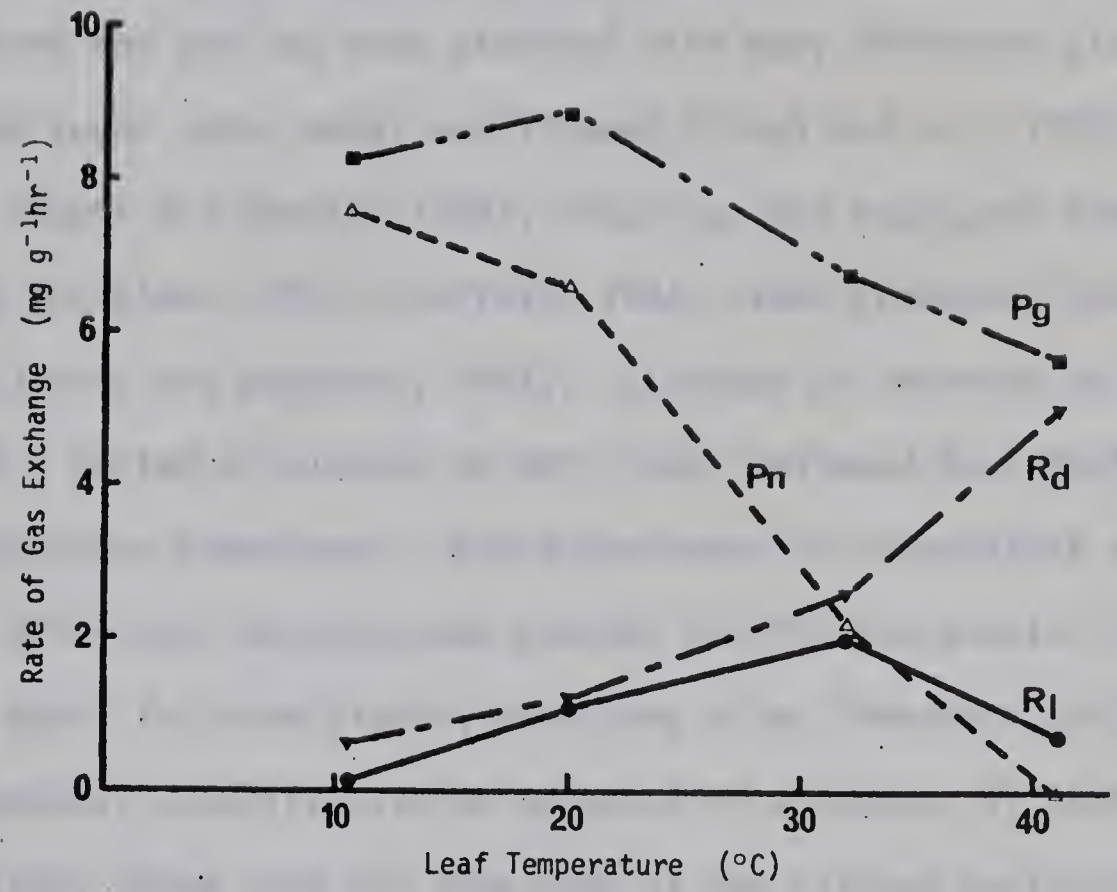


Figure 9. The effect of temperature on the rate of net photosynthesis (Pn), dark respiration (R_d), photorespiration (R_l), and gross photosynthesis (Pg) of a 3-leaved sprig of *Dryas*. Photorespiration was suppressed by measuring the net assimilation rate with air containing 2% O_2. Light intensity: 1000 $\mu E\ m^{-2}sec^{-1}$ (PAR).

THE INFLUENCE OF LEAF AGE ON NET ASSIMILATION

Literature Review

The expected progression of photosynthetic capacity of leaves as they mature and age has been examined with many different plant types including sugar cane, wheat and linseed (Singh and Lal, 1935), *Zelkowa serrata* (Saeki and Nomoto, 1958), *Phaseolus* and *Fagopyrum* (Saeki, 1959), conifers (Freeland, 1952; Stålfelt, 1924, after Freeland, 1952) and a fescue (Jewiss and Wooledge, 1967). It shows an increase to a maximum rate and a period of plateau at this rate, followed by a decline as the leaf approaches senescence. Rapid decreases in chloroplast volumes in tobacco after leaf maturity was reached (Harris and Arnott, 1974) suggest that, for some plants, there may be an immediate decline in photosynthetic capacity with no evidence of a plateau at leaf maturity. Saeki (1959) found that the time span of the plateau period could last from less than a week up to several months, depending on the expected length of leaf life. Collins and Oechel (1974) found that the rates of net assimilation of arctic *Polytrichum alpinum* material which had overwintered were as high at the start of a new season as those exhibited by new tissue. Stålfelt (1924, after Freeland, 1952) found that, with net assimilation rates calculated on a fresh weight basis for the conifers he studied, the peak photosynthetic capacity declined slowly with age over the several following years. He concluded that the rate of net assimilation could remain high for several years. Since the

life span of *Dryas* leaves includes approximately two growing seasons (Svoboda, 1974), it seems that the leaf age studies on conifers (Stålfelt, 1924; Freeland, 1952) are more comparable to *Dryas* than are those on leaves which do not survive a winter.

Results and Discussion

Leaf age does appear to have an effect on the rate of net assimilation by individual leaves of *Dryas* (Fig. 10). This was not at first apparent. In the individual leaf studies, the maximum rates exhibited by first-year leaves and second-year leaves were in the same range and any possible differences in their net photosynthetic capacity were masked by the biological variability between plants. An examination of the contribution of all of the leaves of one sprig to its overall net assimilation balance (Fig. 10) suggests that the net photosynthetic capacity rises to a peak, and then declines as the leaf ages. The highest rate of net assimilation was achieved by a second-year leaf.

In this experiment there were four leaves, the youngest of which had just begun to expand. The oldest leaf showed no signs of senescence. The young second-year leaf had the highest rate of net assimilation (Table 5). The immature leaf showed a net negative assimilation balance at all leaf temperatures greater than 10°C and can therefore be considered a user of, rather than a contributor to the overall carbon balance of the sprig. Although the rate of respiration exhibited by the immature leaf is relatively high (9 mg $g^{-1}hr^{-1}$ at 30°C),

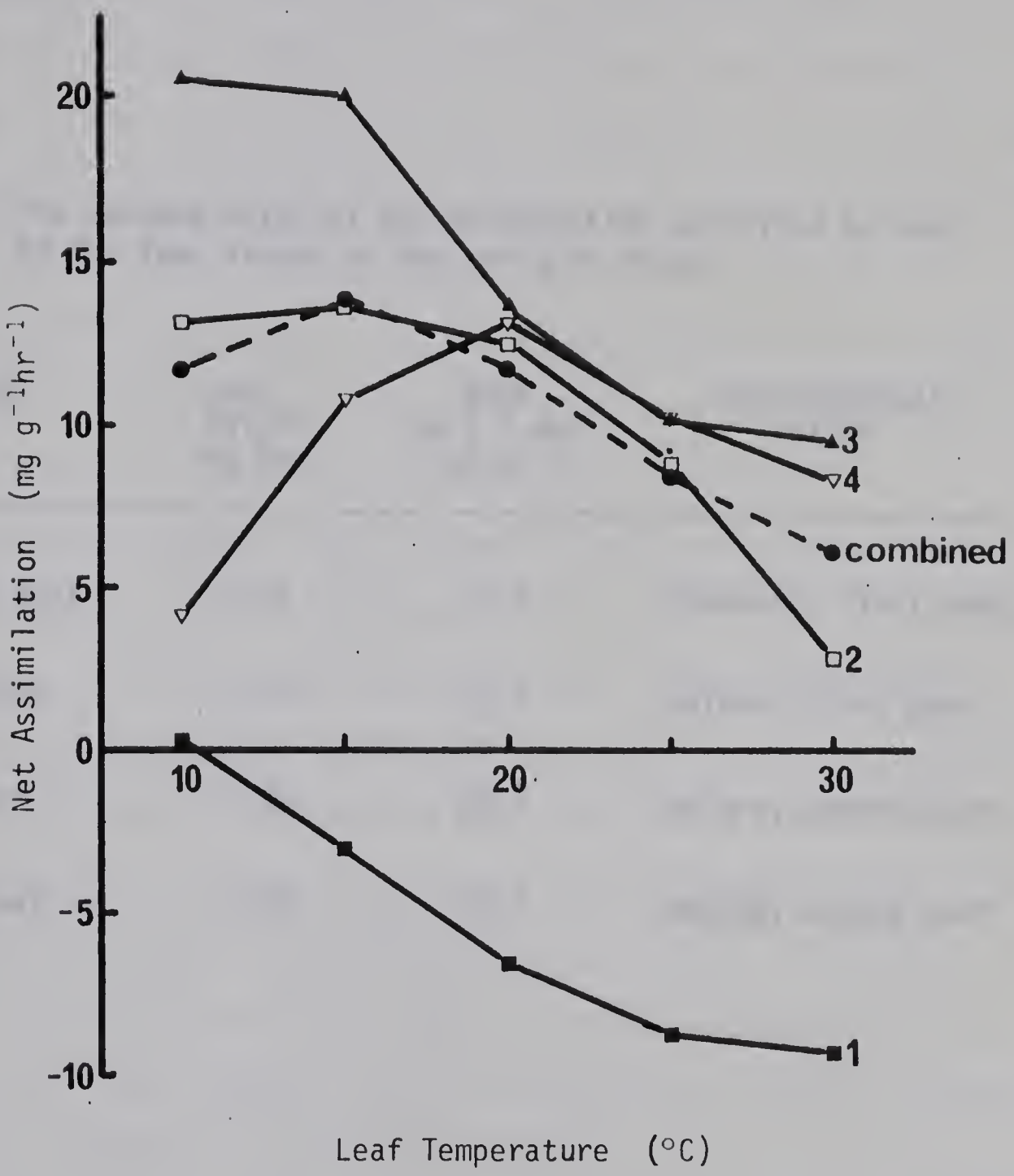


Figure 10. The effect of leaf age on the net assimilation rate by *Dryas* at various temperatures: an examination of the contribution of each of the four leaves of one sprig to the overall net assimilation rate. Light intensity: 900 μE $m^{-2}sec^{-1}$. 1 = youngest leaf, immature; 2 = mature leaf in its first season; 3 = mature second season leaf; 4 = oldest mature second season leaf.

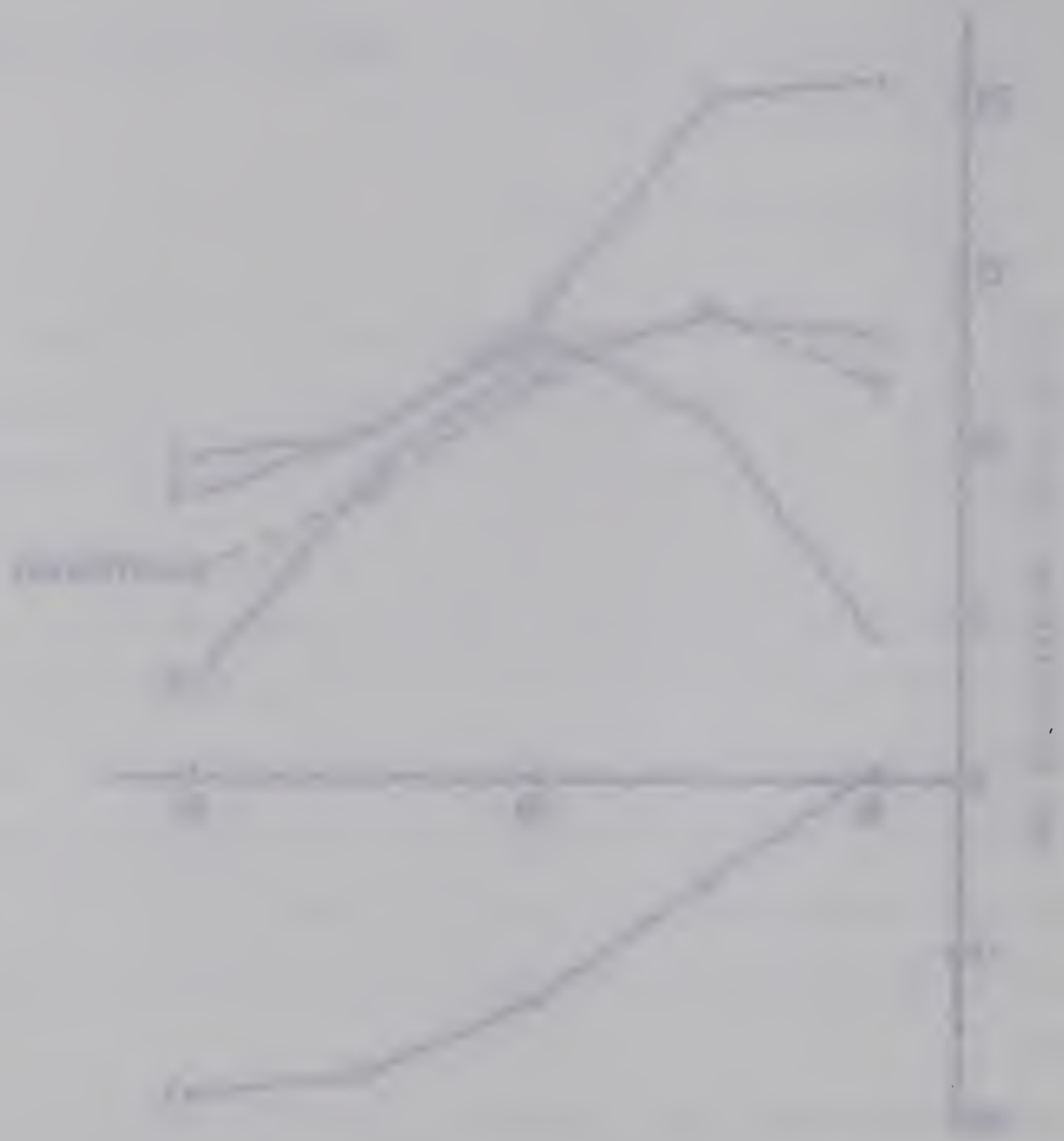


Table 5. The maximum rates of net assimilation exhibited by each of the four leaves in one sprig of *Dryas*.

Leaf	Leaf Weight mg dry	Rate mg g^{-1} dry wt hr^{-1}	Developmental State
Youngest leaf	.029	0.3	immature, first year
Second leaf	.117	13.2	mature, first year
Third leaf	.132	20.7	mature, second year
Fourth leaf	.138	13.7	mature, second year

it is unlikely that this represents much of a drain on the overall net assimilation balance of the sprig since the leaf only makes up 7% of the total dry weight of the sprig. Since there was no discernable difference in the maximum rates of net assimilation of first and second year leaves in the single-leaf experiments, and since the oldest and youngest mature leaves in this experiment were still fixing at a maximum rate of 13 mg $g^{-1}hr^{-1}$, it can be concluded that *Dryas* leaves are active as contributors to the overall net positive assimilation balance for most of their life span when they are mature.

It is more probable that the year in which the maximum rate of net assimilation occurs is determined by the time of initiation of the leaf than by the leaf age as counted in years. The progression of increasing photosynthetic capacity with maturity is somewhat confused by the interuption by a winter and the concurrent reduction of photosynthetic capacity brought about by the onset of dormancy (Fig. 4, p. 30). Since new leaves are continuously being formed, each plant should always have some leaves capable of photosynthesizing at the optimum rate. This idea has also been expressed by Johnson, Caldwell and Tieszen (1974) for several alpine species.

THE EFFECT OF LIGHT INTENSITY ON NET ASSIMILATION

Literature Review

Scott and Billings (1964) concluded that alpine plant productivity was controlled by light intensity at leaf temperatures below 25°C. The amount of light available for photosynthesis can, therefore, be a significant limiting factor to growth over an extended period. Although temperature is more often considered to be the major environmental parameter controlling plant photosynthetic production in the arctic (p. 18), it is still important to understand the photosynthetic response of individual species to variations in light intensity.

The response of net assimilation to light has been studied for a wide range of species. Larcher (1969) has reviewed the literature pertaining to trees, Hesketh and Baker (1967) that pertaining to agricultural plants, and Pisek (1960) that for arctic and alpine plants. The general response patterns of net assimilation to light have been reviewed by Gabrielsen (1960), Hesketh and Moss (1963) and Hesketh and Baker (1967). It has been found that plants can be divided into several groups on the basis of their net assimilation response to light. The first contains the more highly productive C_4 species whose net assimilation apparently does not approach light

saturation within naturally occurring light intensities (>8000 ft-c) and which exhibit very high rates of net assimilation, often in the neighbourhood of 50 mg $dm^{-2}hr^{-1}$ (Table 6). The second group exhibits a photosynthetic light response pattern common to most C_3 species. This is characterized by an obvious approach to light saturation at intensities well below those of full sunlight (Hesketh and Moss, 1963; Gabrielsen, 1960) and maximum rates of net assimilation never much greater than 20 mg $dm^{-2}hr^{-1}$ (Hesketh and Moss, 1963; Böhning and Burnside, 1956). This second group can be further subdivided into sun-adapted plants with somewhat higher light compensation and saturation points and higher rates of net assimilation as opposed to shade-adapted plants which have very low light compensation and saturation points and relatively low maximum rates of net assimilation (Table 6). As stated in the methods (p. 11), many of the values at which photosynthesis is considered to be light saturated as presented in the literature, are based on the subjective opinion of the researcher.

In addition to following one of these generalized patterns, the response of net assimilation of an individual plant to light intensity is affected by leaf temperature. Light compensation points increase exponentially with leaf temperature (Lieth, 1960; Pisek, 1960) due to the exponential rate of increase of respiration with temperature. In contrast to this, the light intensity required to saturate net assimilation does not change much with temperature over a wide range, especially below 30°C (Larcher, 1969; Hadley and Bliss, 1964). The response of net assimilation to irradiance is also affected by

Table 6. Light response characteristics of net assimilation by plants in various groups at 20° to 30°C.

Group	Compensation point ft-c	Saturation point ft-c	Rate mg $g^{-1}hr^{-1}$	Reference
Temperate shade plants	50	≤ 1000	5	Sparling, 1967
Temperate sun plants	50 - 220	≤ 3000	20	Böhning and Burnside, 1956
Shade conifers		≤ 3000		Larcher, 1969
Sun conifers	150	≤ 5000		Larcher, 1969
Alpine and arctic plants	150 - 300	≤ 5000		Appendix C
Many C_4 plants		≥ 8000		Hesketh and Moss, 1963; Chen, Brown and Black, 1969; Hatch, Slack and Bull, 1969

phenology (Larcher, 1969). Young developing leaves have a higher proportion of respiration to photosynthesis than do mature leaves, thereby increasing the amount of illumination they require to achieve light compensation (Hadley and Bliss, 1964).

Most of the data pertaining to the light response of net assimilation of arctic and alpine species has been collected from whole plant or shoot responses and is therefore not fully comparable to the data presented in this study. These data are summarized in Table 7 and presented in greater detail in Appendix C. It appears that the amount of light required for compensation of net assimilation of arctic and alpine species is generally higher than that necessary to achieve the same for temperate and tropical species. This may be due, in part, to the higher rates of respiration exhibited by some cold-climate adapted species (p. 37). Most arctic and alpine species approach light saturated net assimilation at intensities below one half of full sunlight (Table 6), however, there are a few exceptions to this, as can be seen in Table 7.

Results and Discussion

The response of net assimilation of *Dryas integrifolia* to varying light intensity at each of several constant leaf temperatures is presented in Fig. 11 (p. 57). The light compensation point increases exponentially with temperature up to 20°C, as expected, but the increase to 30°C was not as high as would be predicted by an exponential increase (Fig. 12, p. 59). This can be correlated with a similar pattern expressed in the response of both dark respiration and

Table 7. Light response characteristics of net assimilation of some alpine and arctic species.

Group	Compensation point ft-c	Saturation point ft-c	Temperature °C	Reference
Dryas punctata		2000 - 3000	18°	Gerasimenko and Zalensky , 1973
Most arctic and alpine plants	150 - 300	≤ 5000	20°	Appendix C
Geum (alpine, spring)	300	7000 - 9000	20°	Hadley and Bliss, 1964
Thalictrum (arctic)	150 - 300	7000 - 9000	20°	Mooney and Johnson, 1965
Arctic grasses	250	≤ 5000	15°	Tieszen, 1973
Celmisia, Chionochloa	550		20°	Scott, Menalda and Rowley, 1970
Dryas integrifolia	510	9000	20°	this study

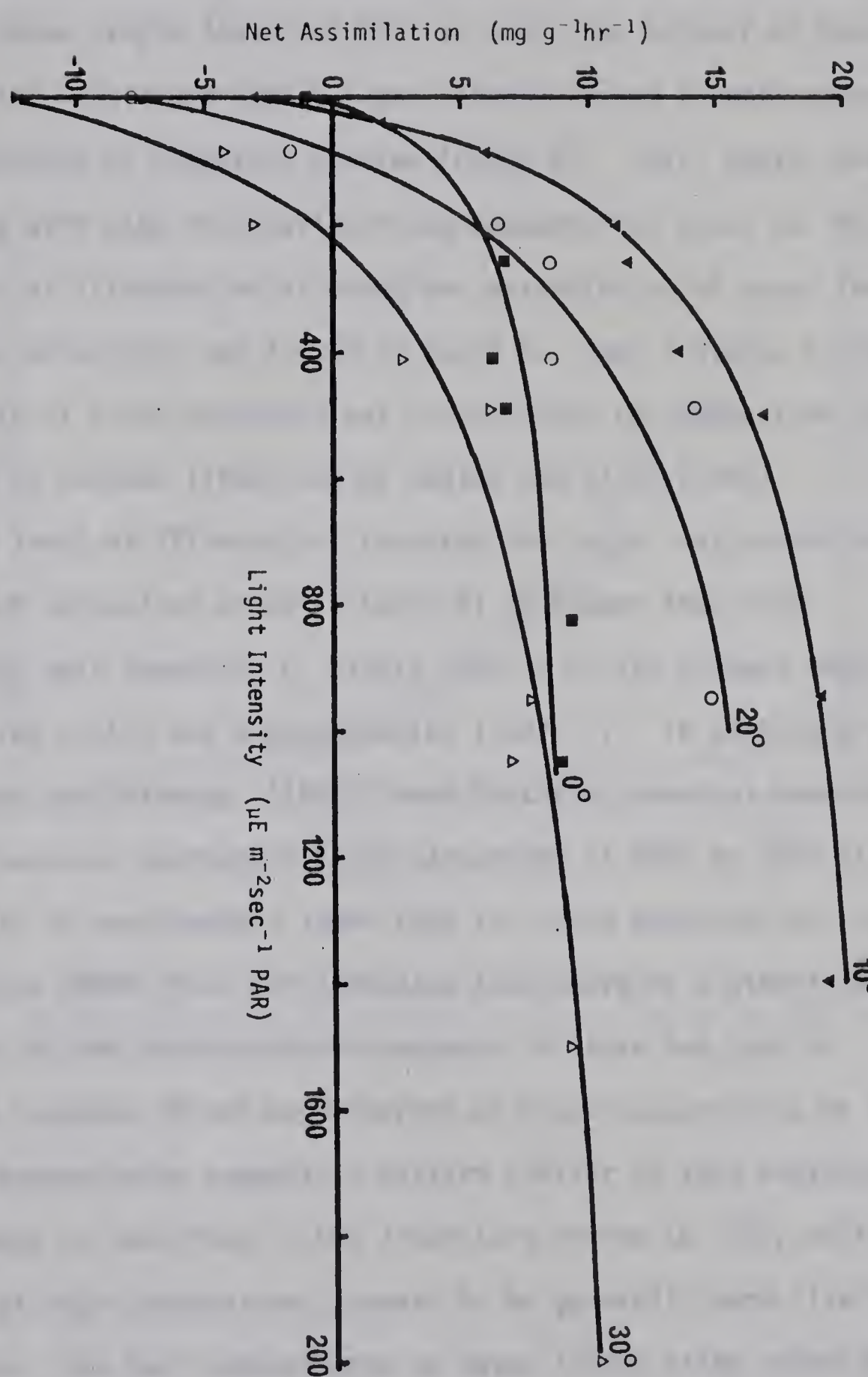
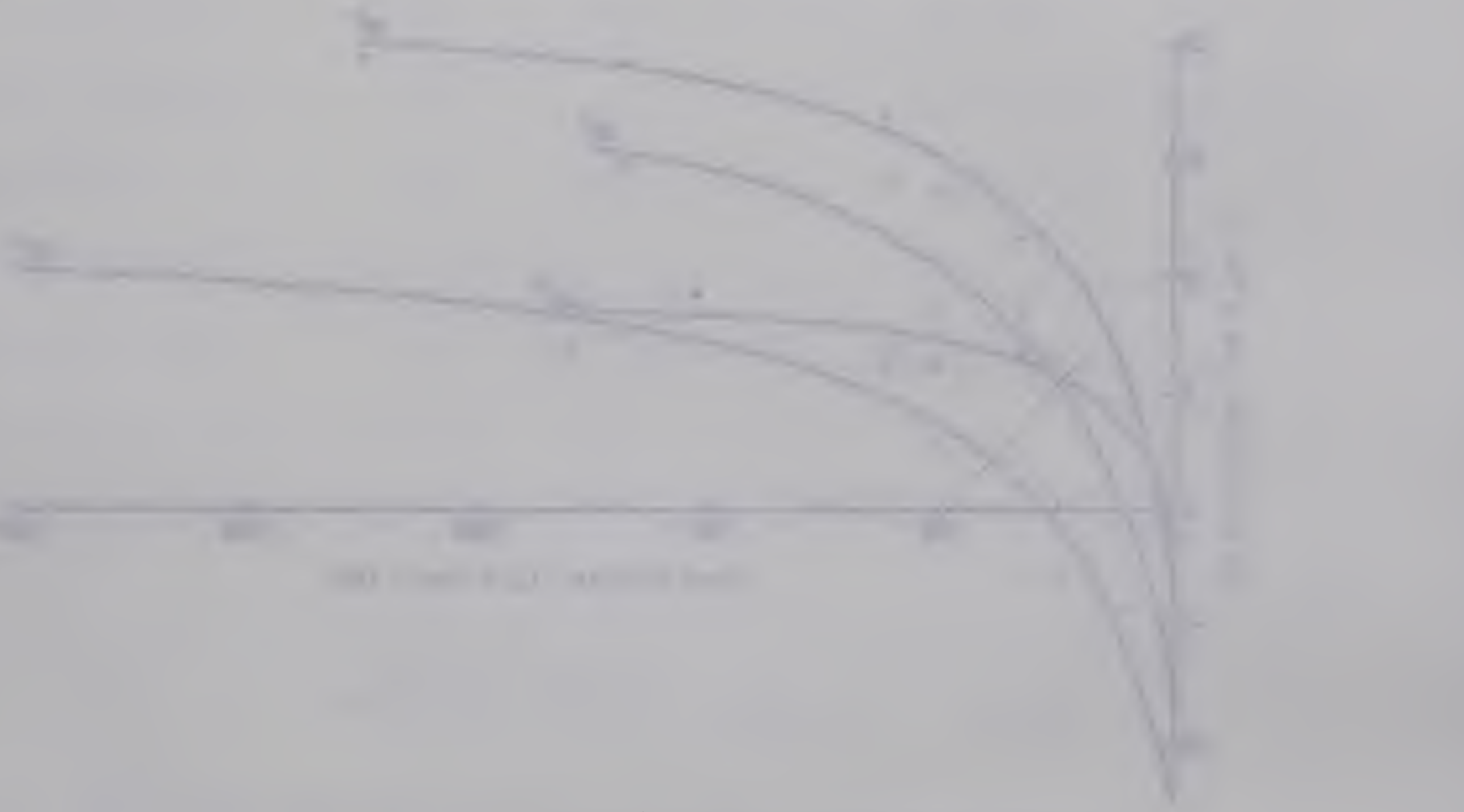


Figure 11. The response of net assimilation by single *Dryas* leaves to light intensity at various leaf temperatures. Curves were fitted mathematically with the equation $Pn = \frac{aL}{bL + 1} - R$ (p. 10). The data points are means of 2 to 7 values. 1 μE $m^{-2}sec^{-1}$ = 60 lux.



photorespiration (Fig. 12) to temperature. The light compensation point of *Dryas* single leaves at 20°C is among the highest of those measured for arctic and alpine plants (Table 7) and is well above those exhibited by temperate species (Table 6). This, again, can be correlated with high respiration rates measured for *Dryas* (p. 40). The levels of illumination at which net assimilation of *Dryas* leaves approaches saturation are listed in Table 8. They indicate a greater sensitivity of light saturated net assimilation to temperature than is suggested by Larcher (1969) and by Hadley and Bliss (1964).

The level of illumination required for *Dryas* net assimilation to approach saturation at 20°C (Table 8) is higher than that required by most temperate C_3 plants, and is in the highest range measured for arctic and alpine species (Table 7). In particular, Gerasimenko and Zalensky (1973) found that the potential photosynthesis of *Dryas punctata* approaches light saturation at 2000 to 3000 ft-c at 18°C. This is considerably lower than the value measured for *Dryas integrifolia* (9000 ft-c). It indicates that there is a significant difference in the photosynthetic response of these two species.

The response of net assimilation of *Dryas integrifolia* to light at low leaf temperatures suggests a pattern similar to that exhibited by shade plants as described in the literature review (p. 53), while the response at high temperatures appears to be generally more like that of sun plants. Low leaf temperatures on Devon Island often coincide with low light intensities (Mayo *et al.*, 1973) so the low light compensation points and rapid rise to saturation below 10°C leaf temperature (Fig. 11)

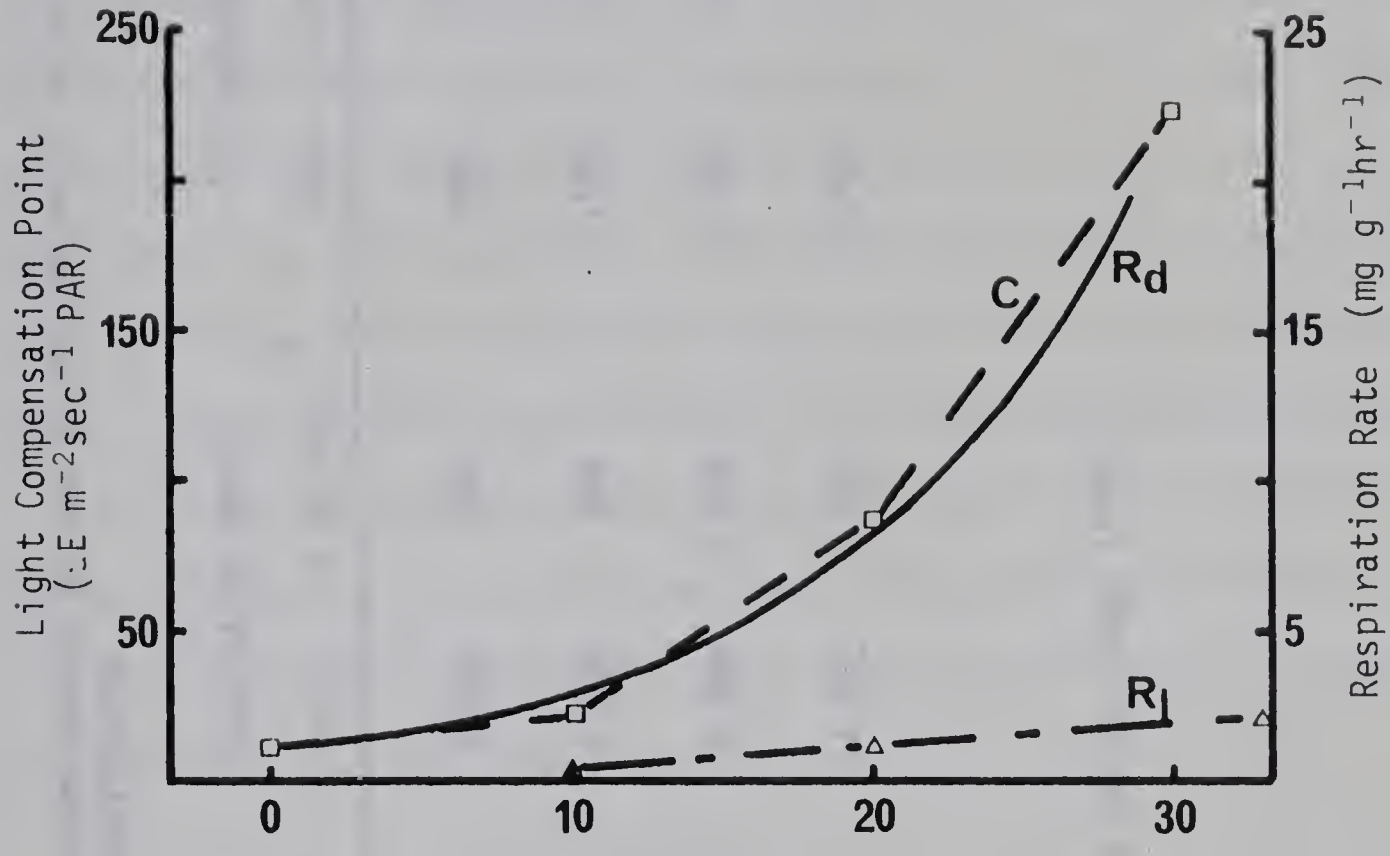


Figure 12. Light compensation points (C), dark respiration (R_d) and photorespiration (R_1) rates by *Dryas* leaves as they are affected by leaf temperature.

Table 8. Light compensation and saturation points of net assimilation of *Dryas integrifolia* at various leaf temperatures.

Temperature	Compensation point		Saturation Point		1/2 Saturation	
°C	ft-c	μE $m^{-2}sec^{-1}$*	ft-c	μE $m^{-2}sec^{-1}$*	ft-c	μE $m^{-2}sec^{-1}$*
0°	70	11.6	3,276	546	660	110
10°	135	22.4	5,394	899	1,140	190
20°	522	87.0	9,468	1,578	1,740	290
30°	1,345	224.2	14,532	2,422	3,420	570

* Light intensities measured in 400 to 700 nm range (PAR).

ensure efficient utilization of the low available light. This condition will occur most frequently during the night when sun angles are low, or on foggy days. It probably accounts for most of the high positive net assimilation measured for *Dryas* in the field during the night period. Leaf temperatures do not rise above 30°C in the field unless the incoming radiation is high (Mayo *et al.*,1973; Biebl, 1968) so the high light compensation point of net assimilation at 30°C is not necessarily a disadvantage. The light response of net assimilation indicates that 10°C is the optimum temperature for net assimilation by *Dryas integrifolia* from Devon Island. The light compensation point is still low, and saturation is approached rapidly with high rates of net assimilation. This reinforces the conclusions drawn from an examination of the response of *Dryas* net assimilation rates to leaf temperature (Fig. 3, p. 26).

WATER RELATIONS OF *DRYAS INTEGRIFOLIA*

Introduction

The water content in plant tissues is usually high (80 to 90%), and even small fluctuations in this amount can result in significant changes in metabolic growth processes (Slatyer, 1967). Many temperate and warm-climate species, especially those used in agriculture, show effects of moisture stress at relatively high water potentials (-2 to -12 bars; Levitt, 1972), and therefore their growth can be expected to be water limited throughout most of the growing season unless they are irrigated. It has been assumed that water plays an even more important role in controlling growth patterns of species found in naturally xeric habitats, as evidenced by the wide variety of physical adaptations evolved by these plants to survive situations of extreme water deficit (Levitt, 1972; Walter, 1973). Oechel, Strain and Odening (1972) concluded that tissue water potential is the most important factor controlling the life processes of *Larrea divaricata* in a desert environment. Water deficits have also been found to limit production in arctic and alpine tundra plants (Stoner and Miller, 1975; Ehleringer and Miller, 1975; Kuramoto and Bliss, 1970).

Arctic plants often experience water deficits (Teeri, 1973; Addison, 1973; Stoner and Miller, 1975) far greater than those which may be injurious to mesic temperate species, although information on the latter is heavily biased by the inclusion of agricultural varieties. *Dryas integrifolia* on Devon Island grows on well drained beach ridges

and is therefore exposed to severe soil drought as the growing season progresses (Addison, 1973). This is reflected in low leaf water potentials (-10 to -53 bars) measured in the field (Addison, 1973). It has been suggested (p. 28) that water status may be an important factor in the reconciliation of the high rates of net assimilation measured under controlled conditions with the low rates observed in the field.

Hsiao (1973) has stated that water potential values *per se* may not be crucial in determining plant behaviour. Courtin and Mayo (1974) have pointed to the lack of information on component water potentials and have stressed the importance of making these measurements, especially in relation to phenology. Some aspects of the water status of *Dryas integrifolia* in relation to rates of net assimilation of CO_2 and transpiration of H_2O, phenology, and tissue water content have therefore been examined in an effort to establish what adaptations *Dryas* might have to withstand the extreme xeric conditions to which it is exposed on Devon Island.

The General and Seasonal Water Status of *Dryas*

Literature Review

Water Potentials

Both Courtin and Mayo (1974) and Hsiao (1973) have pointed out the importance of measuring the components of water potential to give a more complete understanding of plant-environment interactions. Unfortunately, until recently, only total water potentials or xylem

tensions have been measured but seldom both at once. Table 9 illustrates that agricultural species and arctic and alpine grasses and sedges tend to have higher water potentials than those exhibited by trees and shrubs, regardless of habitat. Most agricultural species readily attain water potentials approaching 0 bars under favourable conditions, and many show some inhibition of growth at the maximum leaf water potentials listed in Table 9 (Acedevo, Hsiao and Henderson, 1971; Boyer, 1965 and 1970b), with possible cessation of growth and positive net assimilation at water potentials only slightly below the maximum (-10 bars) observed for arctic shrubs (Table 11, p. 95). In contrast to this, more xerophytic species such as some arctic, alpine and desert shrubs are able to assimilate CO_2 at much lower water potentials (Table 11, p. 95).

The Importance of Turgor Pressure

It has been established that turgor pressure is an important factor in the cell expansion phase of growth (Cleland, 1971; Vaadia, Raney and Hagan, 1961; Green, 1968) and that there is a threshold pressure below which cell expansion will not occur (Kirkham, Gardner and Gerloff, 1972). Other aspects of growth, however, are not so dependent on turgor pressure, as is evidenced by the photochemical activity of chloroplasts at water potentials below that at which turgor reaches 0 (Boyer and Potter, 1973), and by continued incorporation of DNA when cell expansion had stopped (Kirkham, Gardner and Gerloff, 1972). Acedevo *et al.* (1971) have suggested a possibility for "stored growth" which could make up for short periods of no elongation due to water

Table 9a. Maximum and minimum water potentials of various cultivated species.

Species	Water potentials in bars				Reference
	Maximum		Minimum		
	Ψ*	$\Psi_{\pi+\tau}$*	Ψ	$\Psi_{\pi+\tau}$	
Pepper	-2	-8 to -10	-22	-22	Gardner and Ehlig, 1965
Soybean	-2.5		-17		Teare and Kanemasu, 1972
Sunflower	-2	-8	-10	-10	Boyer and Potter, 1973
"			-16		Boyer, 1971
"	-4	-10	-22.4	-22.4	Gardner and Ehlig, 1965
Sorghum	-4		-22		Turner, 1974
Beta vulgaris	-4		-14		Biscoe, 1972
Trefoil	-6	-11	-20.3	-20.3	Gardner and Ehlig, 1965
Tobacco	-6		-15		Turner, 1974
Maize	-7		-18		Turner, 1974
Cotton	-8	-12	-19	-19	Gardner and Ehlig, 1965

* Ψ = total water potential, $\Psi_{\pi+\tau}$ = combined osmotic and matric potential.

Table 9b. Maximum and minimum water potentials of non-cultivars.

Species	Water potentials in bars				Reference
	Maximum		Minimum		
	Ψ*	$\Psi_{\pi+\tau}$*	Ψ	$\Psi_{\pi+\tau}$	
Red pine		-4.2		-18	Sucoff, 1972
Arctic plants	-1 to -2		-7 to -12		Stoner and Miller, 1975
Arctic and alpine graminoids	0 to -8				Courtin and Mayo, 1974
Alpine plants	-1 to -10		-17 to -40		Ehleringer and Miller, 1975
Bog species		-12 to -19			Small, 1972
Dryas integrifolia	-10		-50		Addison, 1973
Saxifraga	-10				Teeri, 1973
Dryas octopetala		-13.3		-18.3	Pisek, Sohm and Cartellieri, 1935
Picea spp.	-13 to -17	-15 to -26			Courtin and Mayo, 1974
Larrea divaricata		-24.6		-40	Oechel *et al.*, 1972
Carex rariflora	-25				Haag, 1972
Eriophorum russeolum	-35				Haag, 1972

* Ψ = total water potential, $\Psi_{\pi+\tau}$ = combined osmotic and matric potential.

stress by a rapid phase of growth after alleviation of the stress. This indicates that some metabolic events related to growth may continue when turgor falls below the expansion threshold. There is also some evidence for a readjustment of the threshold turgor required to effect cell expansion under conditions of prolonged water deficit (Green, 1968; Green, Erickson and Buggy, 1971). It is agreed that for continued growth, there must be some turgor pressure in the cells. The ability or lack thereof of cells to maintain turgor over a range of water potentials or water contents must therefore be of considerable importance to their capacity for survival or growth during long periods of water deficit.

There is evidence that at least some types of cells are able to adjust osmotically to a decrease in water availability, thereby maintaining a certain degree of turgor (Hsiao, 1973). This ability was observed in root cells (Greacen and Oh, 1972) and in cotton (Boyer, 1965) but not in *Nitella* (Green, 1968) or in *Avena* coleoptiles (Cleland, 1971). Adjustments in the required turgor threshold or in cell wall extensibility (Hsiao, 1973) may be as important in allowing resumption of growth but these would not suffice if turgor pressure should fall to 0.

Water Potential as Related to Water Content

Both Walter (1931, after Walter and Kreeb, 1970) and Höfler (1920) originally suggested a pattern of change of the osmotic and turgor components related to relative cell volume and therefore to water content as determined by the degree of elasticity of the cell walls. The theory was that cells with rigid walls would exhibit a substantial decrease in turgor pressure with a small decrease in volume and there-

fore with a concurrently small decrease in the osmotic potential. Cells with more elastic cell walls would exhibit a smaller decrease in turgor with a similar change in cell volume and therefore, a larger decrease in osmotic potential relative to the decrease in turgor than those with rigid cell walls. Walter (1931, after Walter and Kreeb, 1970) considered the occurence of rigid cell walls to be a water conserving mechanism. Jarvis and Jarvis (1963) observed that this condition did seem to be more prevalent among leaves of xeromorphic than of mesomorphic species. This idea has also been supported by Zavitkovski and Ferrel (1968, after Zavitkovski and Ferrel, 1970) with ecotypes of Douglas fir.

More recently, the observation has been made on a number of agricultural species that cell turgor declines with relative water content in two distinct linear phases characterized by an initial rapid decline to a turgor of about 2 bars, followed by a slow decline to 0 bars (Gardner and Ehlig, 1965). This was attributed to an abrupt change in the elasticity of the cell walls at the point of change, and is reflected in a characteristic response of water potential to relative water content which was also observed by Janes (1970). Warren Wilson (1967a) found that sunflower and rape tissue did not show this change in cell wall elasticity, as the turgor decreased linearly with relative water content until it reached 0. He did, however, (1967b) find that the coefficient of enlargement of the cells tended to increase with drier growing conditions in conjunction with a trend of decrease in the osmotic and matric potentials. This combination served to allow the development of a low water potential at zero turgor without a lowering of the relative water content at this point, which might damage the cells.

The Effect of Phenology on Water Status

Phenology has been shown to affect a number of different aspects of plant water relations, although little work has been reported in this area. Kassam and Elston (1974) have provided evidence for an age-related decline in the water potential, the coefficient of cell enlargement, and the osmotic potential and relative water content at which turgor reaches 0 bars in *Vicia faba*. Pharis (1967) found that foliage moisture content of well watered conifers decreases with needle age, becoming less with each successive summer. He also noted a decrease in the moisture content of the needles in winter as compared to that in summer. Lindsay (1971) also observed that leaf water potentials of *Picea engelmannii* and *Abies lasiocarpa* decreased in winter, although the degree of exposure to cold and wind also influenced the moisture status of these trees. In contrast to this, Sucoff (1972) found that needle age did not affect water potential in *Pinus resinosa*. Ehleringer and Miller (1975) found that the water potentials of alpine herbs and graminoids decreased throughout the summer, while the midday leaf water potentials of arctic graminoids showed no such decreasing trend from June through August (Stoner and Miller, 1975). Walter and Kreeb (1970) illustrate seasonal decreases in the osmotic potentials of many species, and this appears to be the general rule, especially in species with persistent leaves. Many of these decreases may be just a reflection of decreased availability of water as the season progresses.

There is some evidence for an effect of the degree of cold hardiness (Christersson, 1972) and leaf age (Holmgren, Jarvis and Jarvis,

1965; Brown and Rosenberg, 1970; Hailey *et al.*, 1973) on leaf resistance to vapour loss although the latter was not observed by Ehrler and van Bavel (1968). Kozlowski's (1943) observation of a decline in the rate of transpiration throughout the dormant season in some forest trees may be related as much to direct temperature effects as to phenological changes in leaf resistance. Populations of species growing in different areas may exhibit different leaf resistance values under similar conditions (Pearcy and Harrison, 1974). These observations serve to point out that any discussion of plant water relations which is in any way related to a species' capacity for survival in a natural environment must take phenology into account.

Results and Discussion

Water Potential and its Components

The water potentials measured for actively growing *Dryas integrifolia* leaf tissue ranges from -5 to -18 bars with a mean of -11.4 bars (Fig. 13). Values higher than -7 bars were infrequently measured. The data is intermediate between the two extremes shown by water potential values cited in the literature for a number of agricultural and non-agricultural species (Table 9b, p. 66). Some arctic species may have water potentials as high as -2 bars (Stoner and Miller, 1975). *Dryas integrifolia* growing on Devon Island had much lower water potentials than did the laboratory grown plants (Addison, 1973; Table 9b).

Dryas was able to maintain a high turgor pressure (+6 to +10 bars) over the full range of water potentials observed under summer conditions

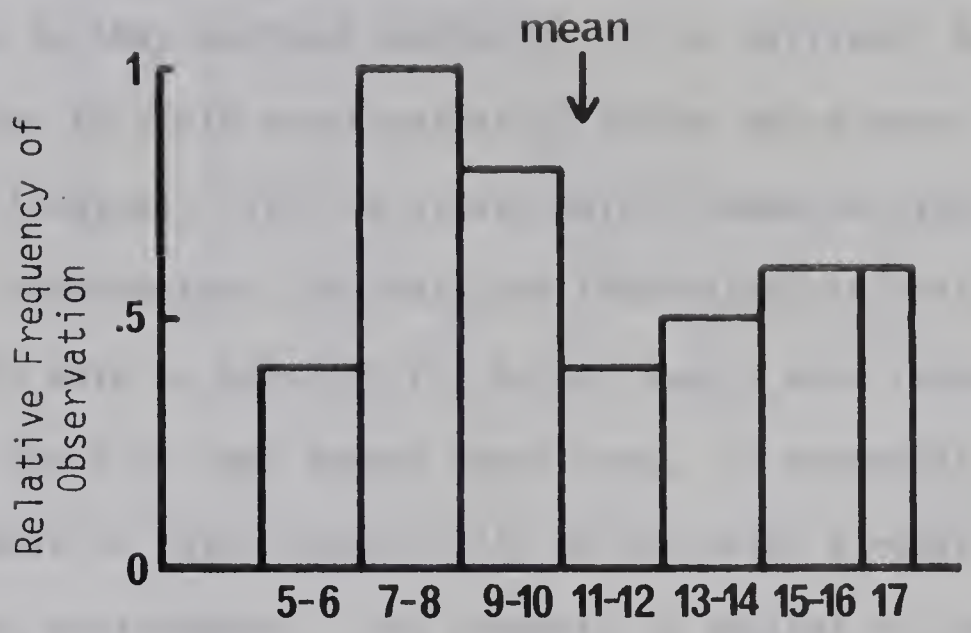
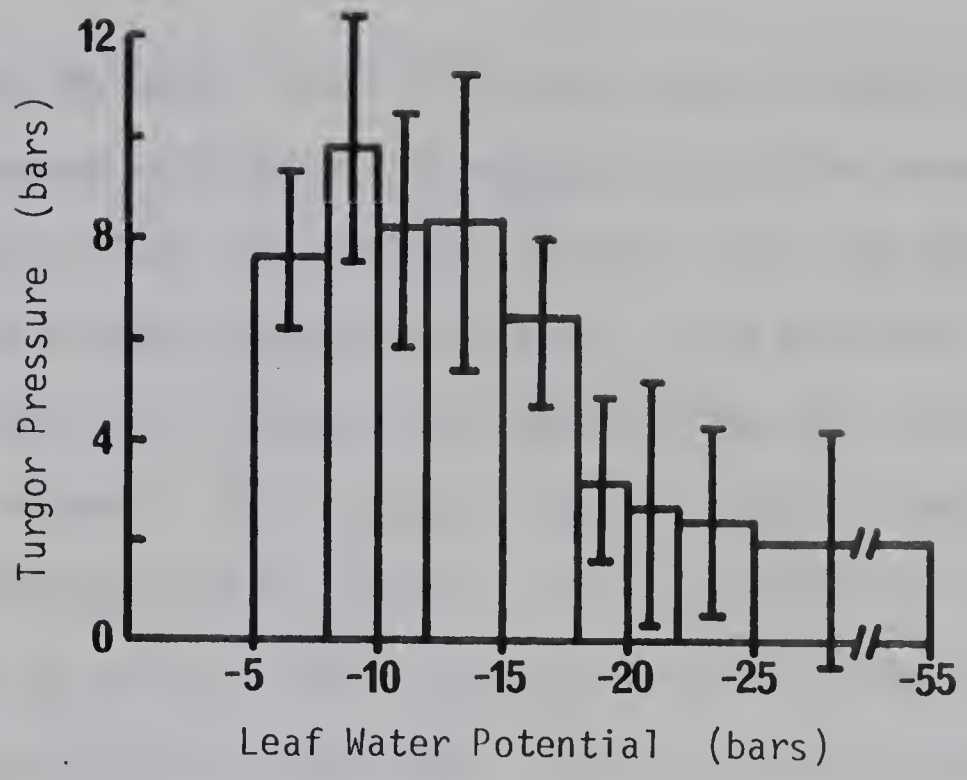


Figure 13. The frequency of observation of various water potential values (Ψ) of non-dormant *Dryas* leaf tissue.

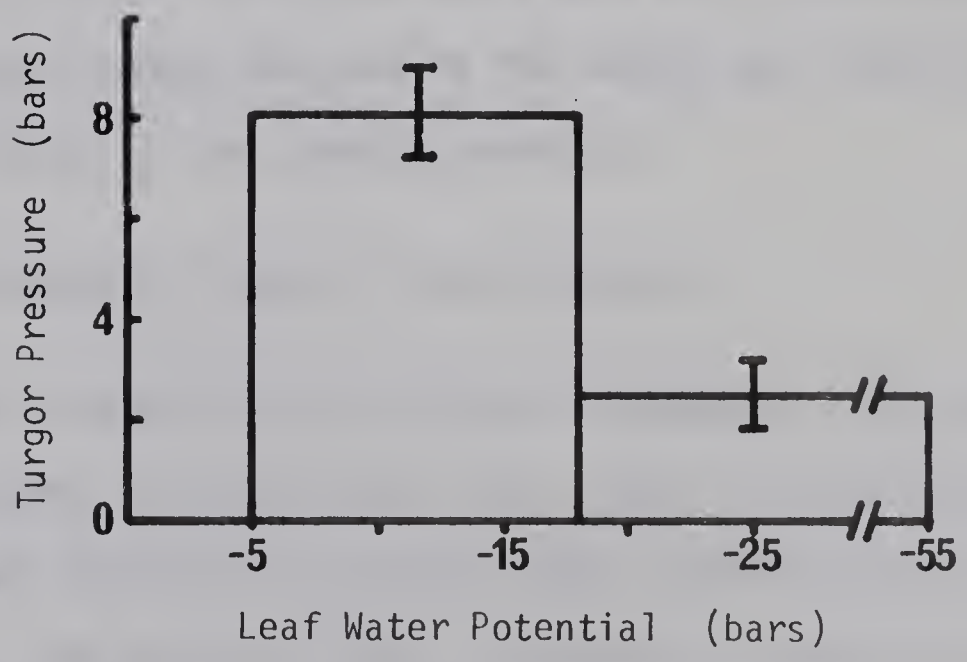
Maximum Ψ on non-dormant tissue	-5.1 bars
Minimum Ψ on " "	-18.0 bars
Mean Ψ on " "	-11.4 bars
Minimum Ψ on dormant tissue	-54.0 bars

in the laboratory (Fig. 14a). The differences in turgor with various total water potentials were not significant until the total water potentials fell below -18 bars (Fig. 14b). Since water potentials below -20 bars were seldom observed in non-dormant tissue, the sudden decrease in turgor pressure at this point may be due to phenological changes in the plants as they approach dormancy. It is difficult to relate this information to field water potential values which were often below -20 bars (Addison, 1973) in plants which showed no signs of impending dormancy. Nevertheless, the data are interesting in that they suggest that *Dryas* is able to maintain its turgor over a wide range of water potentials, at least to some degree above zero. To accomplish this, *Dryas* must be able to adjust osmotically to the water stresses imposed upon it by the environment. This property is unusual in leaves of mesophytic temperate species (Hsiao, 1973). It also suggests that *Dryas* cell walls must be elastic in the sense described by Walter (1931, after Walter and Kreeb, 1970) and Höfler (1920) as discussed in the literature review (p. 67). The ability of *Dryas* to maintain a constant turgor was demonstrated repeatedly, as will be shown in later sections of this chapter.

Since turgor is so important to growth in plants (literature review, p. 64) and since *Dryas* grows relatively slowly (Svoboda, 1974) in a xeric environment with a short growing season, this ability to maintain turgor may be important to enable *Dryas* to achieve enough growth to maintain itself.



a) The data are conbined into intervals of 2 or 3 bars each



b) The data are combined into two groups, one with values above and one with values below -18 bars.

Figure 14. The relationship of turgor pressure (Ψ_p) to the total water potential (Ψ) of *Dryas* leaves. Water potentials of less than -18 bars were measured on tissue which was dormant or approaching dormancy. The confidence intervals are at 95%.

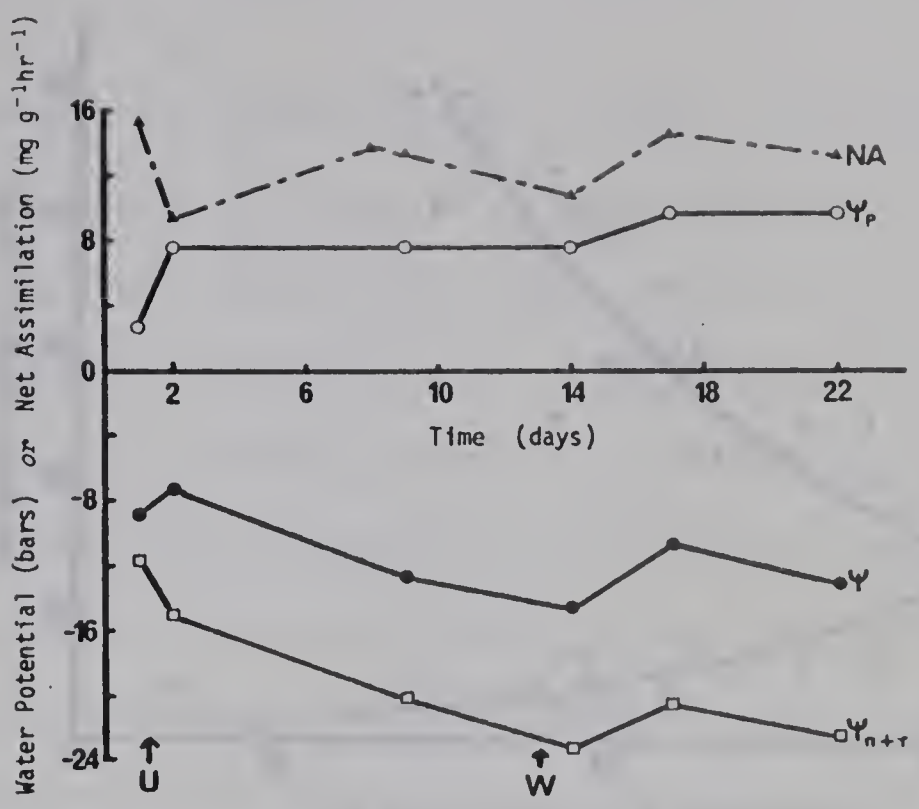
The Effect of High Humidity on Water Potential

Fig. 15b shows the water status of a plant which was kept in well-watered soil and covered with plastic to maintain saturation around the shoots. It is apparent that this treatment did not cause the water potential to rise to a value approaching 0 bars, as was expected. The water potential of the tissue actually decreased during this treatment (from -10.3 to -15.4 bars). This response, coupled with the long delay in water potential response of dry plants to soil irrigation on the 13th day (Fig. 15a) must be due to a high resistance to water uptake somewhere in the system, possibly in the roots. This resistance in *Dryas* to achieving high water potentials may be a mechanism for maintaining some degree of cold hardiness throughout the summer.

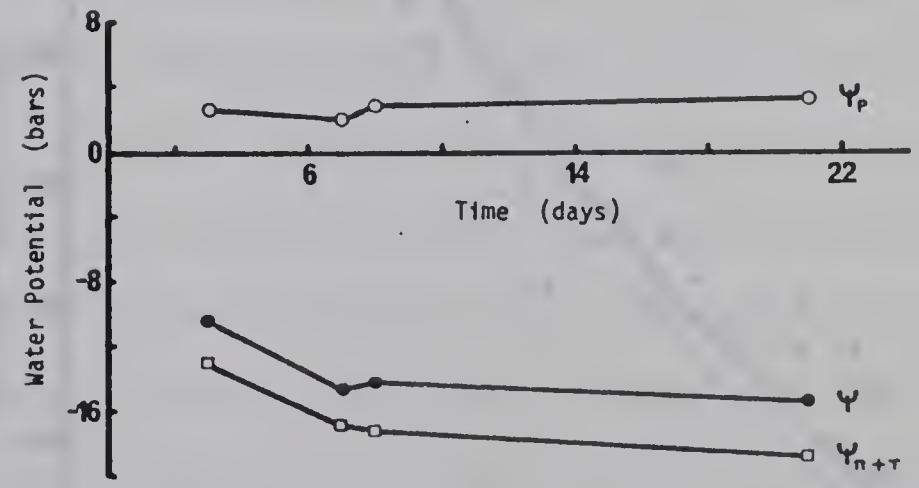
Both Figs 15a and 15b illustrate again that *Dryas* has the ability to maintain a constant turgor pressure in its leaves over long periods of time and with changes in the osmotic potential.

Water Potential Response to Changes in Water Content

The pattern of change of water potential components with water content of *Dryas* leaves is shown in Fig. 16. There is a rapid decrease in osmotic potential relative to a stable turgor over the range of 55 to 70% water content. The ability of *Dryas* to maintain a turgor of 3 to 4 bars over such a wide range of water contents is remarkable and suggests that *Dryas* cell walls must be extremely elastic. Since *Dryas* survives relatively xeric conditions, this is opposite to what one would expect if Walter's (1931) theory that xerophytic species must have rigid cell

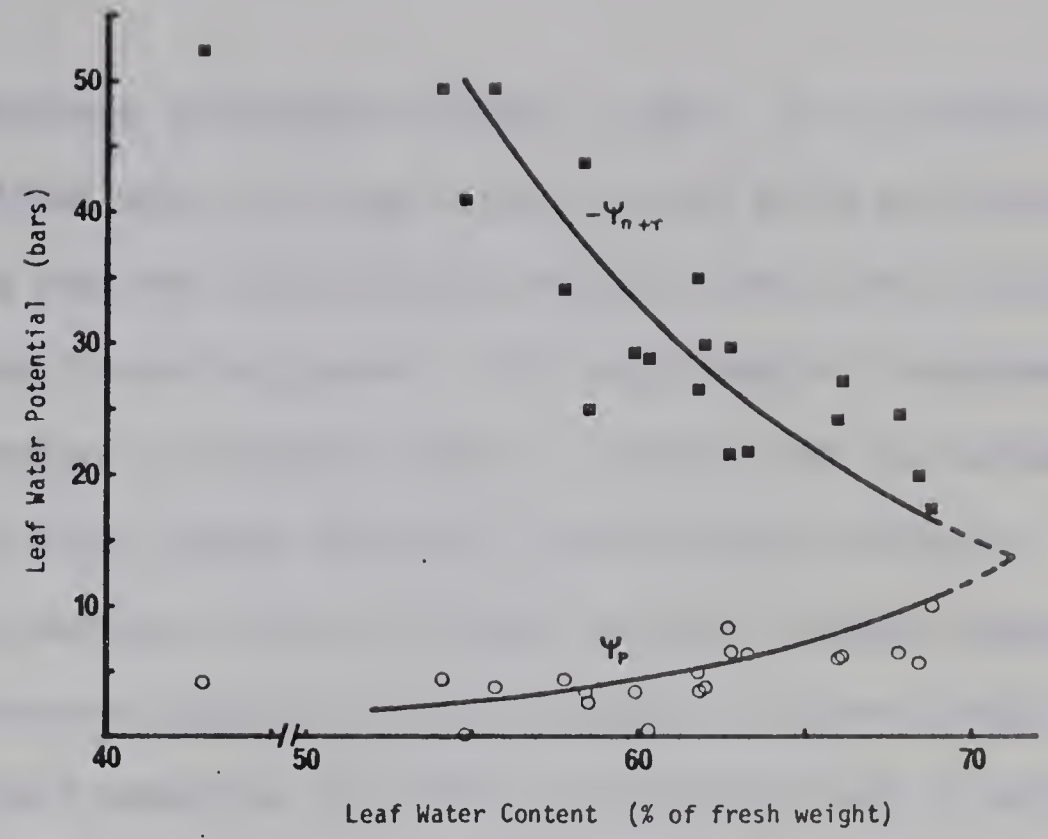


a) Plant had been covered with plastic for several days before the start of the experiment, and uncovered (U) on the first day. Net assimilation by one leaf was followed (NA). W = plant was watered.

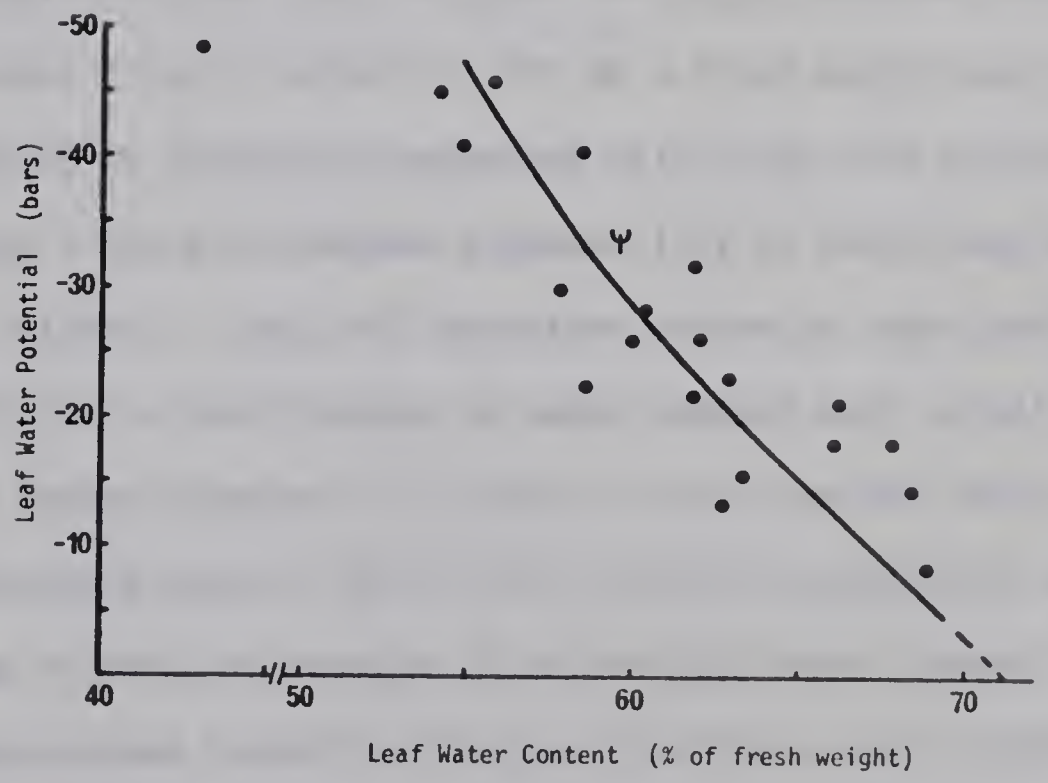


b) Plant as in a) but kept covered with plastic and well watered for the duration of the experiment.

Figure 15. The progression of leaf water potential (Ψ) and its components ($\Psi_{\pi+\tau}$ = osmotic plus matric potential, Ψ_p = turgor pressure) over a three week period during the growing (non-dormant) period. Leaf temperature: 13.5°C; light intensity: 460 μE $m^{-2}sec^{-1}$ (PAR).



a) Component potentials: osmotic and matric ($\Psi_{\pi+\tau}$) and turgor (Ψ_p).



b) Total water potential (Ψ).

Figure 16. Leaf water potential as related to changes in leaf water content at 15.5°C. Cut shoots were placed in various concentrations of mannitol (Ψ = 0 to -6 bars) to effect these changes.

walls is correct (literature review, p. 68). It is possible that much of the initial water lost was stored in cell walls and intercellular spaces, so that the actual water content of the cells did not change much as the tissue lost water. This would enable a maintenance of turgor pressure in inelastic cells. However, the low maximum water content of *Dryas* tissue makes this possibilitity unlikely.

The response pattern of turgor to water content suggests that turgor decreases rapidly with small changes in water content at values close to full hydration (Fig. 16a) and that the rate of decrease is much less at lower hydration levels. This is similar to the two-phase response observed by Gardner and Ehlig (1965). This pattern can be readily explained with the idea that for *Dryas*, maximum hydration occurs around a water content of 70% on a fresh weight basis (Fig. 16). As this point is reached by hydrating cells, the cell walls must be approaching a point of maximum extensibility at which they will no longer be elastic. They will therefore behave as rigid cell walls with the result that a small change in water content must result in a large change in turgor pressure. As water is lost from the cells, the walls are increasingly able to exhibit their elastic properties, as shown by the change in rate of decrease of turgor with water content.

The apparent inability of *Dryas* to achieve water potentials close to 0 bars may be a product of the physical characteristics of *Dryas* cells, in that there is a large difference (Fig. 16) between the osmotic and turgor components at a hydration (69%) approaching the proposed maximum. There may be such a great drop in turgor with a small drop in water content from the maximum that this would inevitably occur during

the space of time required to cut the tissue, weigh it, and place it into a psychrometer. In other types of tissue, this drop may not be so precipitous, so that water potentials approaching 0 bars are more likely to be measured. This possibility is supported by Tinklin and Weatherley (1966). It should be noted, however, that increases in the water potential of cut tissue as compared with that of uncut tissue have been observed (Barrs and Kramer, 1969; Talbot, Tyree and Dainty, 1975). This may be due to reabsorption of water from the cut cells (Barrs *et al.*, 1970). Such a condition might therefore counter decreases in water potential due to evaporative loss after the leaves have been cut from the plant.

Water Potential as Affected by Phenology

The progression of water potential changes in tissue coming out of or entering dormancy is shown in Figs 17 and 18. Although the data is somewhat limited, there does appear to be a trend of decreasing osmotic and turgor components as dormancy is approached (Fig. 17). The response of tissue water status to soil irrigation also appears to change as dormancy is approached in that water applied during the initial stages (day 4) was reflected in an increase of osmotic potential, indicating water uptake. Water applied several weeks later (day 23) caused no increase in either the osmotic or the turgor components. This suggests a change in the plants' capacity for water uptake. Insensitivity to available water in the latter stages of induction of dormancy could be important to ensure the achievement of winter hardiness. The decrease in the water potential is probably a reflection of winter hardiness and

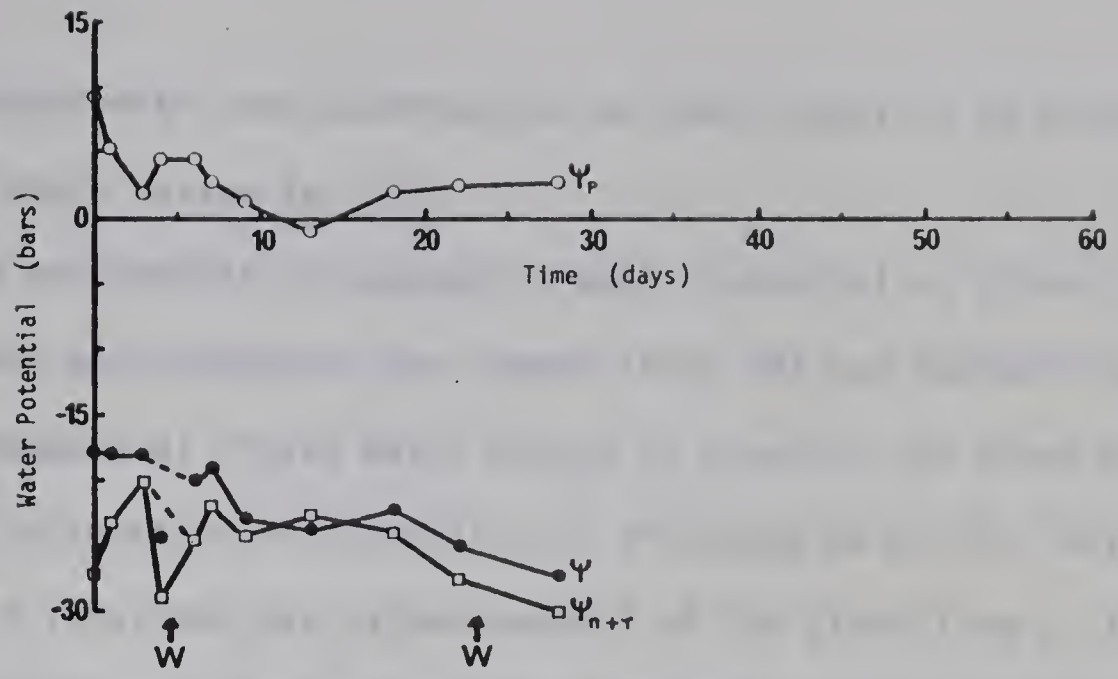


Figure 17. The progression of change in the components of leaf water potential (osmotic and matric: $\Psi_{\pi+\tau}$, turgor: Ψ_p, total water potential: Ψ) with time as plants enter dormancy. Temperature was decreased from -1° to -7°C. W = plant was watered.

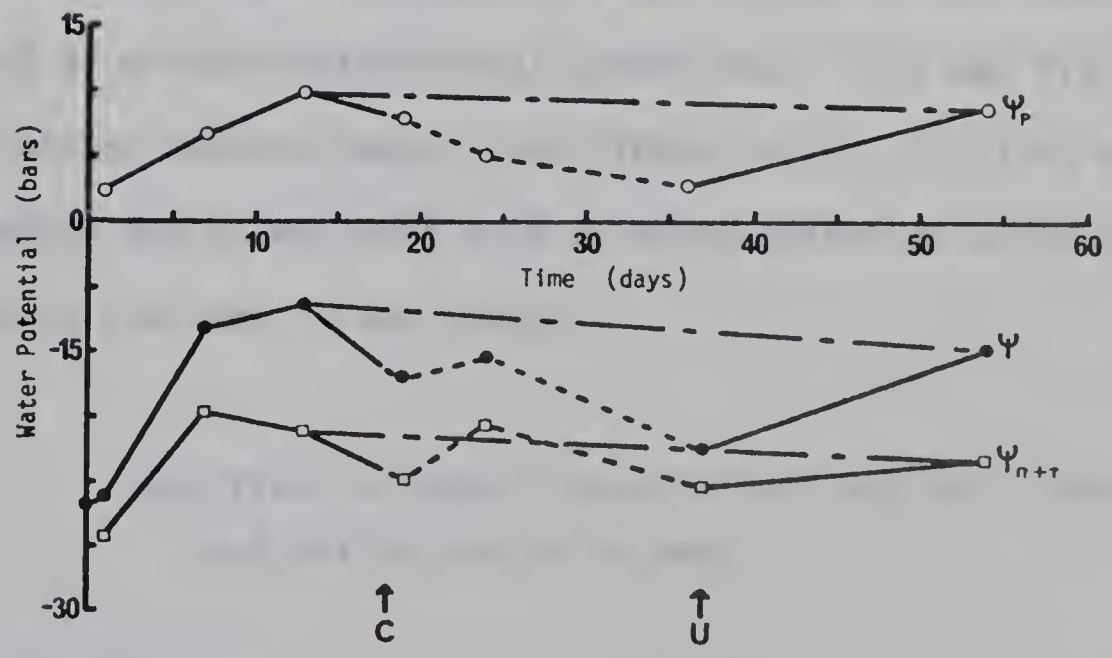


Figure 18. The progression of change in the components of leaf water potential with time as plants come out of dormancy. Temperature in dormancy: -4°C, increased from 1° to 8°C during the first week, then the normal summer temperature regime was followed (fluctuating 0° to 10°C). C = plant covered with plastic; U = plant uncovered from plastic. The effect of plastic cover is to increase air humidity around the leaves, and to decrease the turgor pressure in the leaves.

is consistent with such observations on other species, as presented in the literature review (p. 69).

The measurement of changes in water potential as plants come out of dormancy and throughout the summer (Fig. 18) was somewhat confounded by the response of tissue water status to covering the plant with plastic in order to increase the humidity, as discussed on p. 74. Nevertheless, during the first ten days after removal of the plant from a simulated winter environment, turgor pressure increased to its normal active-tissue value of +8 to +10 bars (Fig. 18, Fig. 14, p. 73), osmotic potential increased to between -15 and -20 bars, and as a result, water potentials fell to within the normal summer range (-7 to -18 bars) observed for laboratory grown plants. It is apparent from this data that a return to the summer state of water status is not immediate upon the removal of winter environmental conditions. This may fit in with the observations made on Devon Island (Mayo *et al.*, 1973) of a several day lag before the plants were able to photosynthesize after they had melted out of the snow in the spring.

The Effect of Water Potential on Leaf Resistance and Net Assimilation Rate

Literature Review

Leaf Resistance

The regulation of stomatal or leaf resistance to diffusion of carbon dioxide is important to the survival of species in certain

habitats. Most agricultural species exhibit low minimum leaf resistances (Table 10) while leaves of conifers and other xeromorphic species, specifically the water-savers in Levitt's terminology (1972), tend to have higher minimum leaf resistances to diffusion of water and carbon dioxide.

Leaf resistance to water loss has been found to remain constant over a wide range of decreasing water potentials until a threshold is reached below which the resistance increases sharply (Beadle *et al.*, 1973; Jordan and Ritchie, 1971; Kanemasu and Tanner, 1969). This threshold is associated with stomatal closure. Biscoe (1972) has suggested that this response is an artifact of rapid experimental treatment and that plants stressed slowly over a period of days will exhibit a close relationship of leaf resistance with water potential at all times. Zabadal (1974) has found that abscisic acid increased in *Ambrosia* within a critical water potential range of -10 to -12 atm which corresponds to the threshold value for increase in leaf resistance observed for many species. Abscisic acid has been shown to increase with water deficit (Wright and Hiron, 1969; Dörffling, Sŏnka and Tietz, 1974) and is involved in promoting stomatal closure (Mittelheuser and van Steveninck, 1969; Horton, 1971). It therefore seems possible that the pattern of change of leaf resistance with decreasing water potential is dependent on changes in concentration of abscisic acid in the tissue.

Stomatal opening, and therefore leaf resistance, is also controlled by several other parameters such as light, temperature and the concentration of CO_2 or H_2O in the atmosphere. Stomata generally

Table 10. Minimum and maximum leaf resistances to water loss measured on various plant groups.

Plant group	Leaf resistance sec cm^{-1} Minimum	Maximum	Reference*
Cultivated species	0.5 to 3	6 to 52	(2), (3), (6), (7), (11)
Dryas integrifolia	1.8 to 4.9	20.4	(1)
Alpine herbs	0.8 to 1.6	4 to 11	(5)
Arctic species	1 to 3	30 to 40	(10)
Arctophila fulva	6	40	(10)
Shrubs	1 to 13		(8), (9)
Deciduous trees	1.2 to 20	21 to 58	(4), (7), (8), (9)
mean	8.5		
Shade herbs	7.6 to 9.2		(7)
Conifers	20 to 45		(8)

*(1) Addison, 1973
(2) Al Ani and Bierhuizen, 1971
(3) Biscoe, 1972
(4) Davies and Kozlowski, 1974
(5) Ehleringer and Miller, 1975
(6) Ehrler and van Bavel, 1968
(7) Holmgren, Jarvis and Jarvis, 1965
(8) Miller and Gates, 1967
(9) Small, 1972
(10) Stoner and Miller, 1975
(11) Turner, 1974

open in the light and close in the dark (Meidner and Mansfield, 1968; Slatyer and Bierhuizen, 1964). The degree and rapidity of this response varies with species and may be overridden by endogenous rhythms (Meidner and Mansfield, 1965) and by other environmental factors usually relating to water status. The reader is referred to Meidner and Mansfield (1965) for a complete discussion of this phenomenon and to Hsiao (1973) and Meidner and Mansfield (1968) for a discussion of leaf resistance response to the environmental parameters which have not been examined in this study.

The Effect of Water Potential on Net Assimilation

The effect of water status on net assimilation rates is often indirect, through the response of stomata altering leaf resistance to diffusion of CO_2 (Boyer, 1971; Jones, 1973; Brix, 1962). There is also some evidence for a nonstomatal effect of water stress on net CO_2 assimilation by changes in the mesophyll resistance to CO_2 uptake (Redshaw and Meidner, 1972; Hsiao, 1973; Drew, Drew and Fritts, 1972; Boyer and Bowen, 1970). This evidence, however, is tenuous, and it has been concluded that moderate water stress exerts its effect on net assimilation rates almost completely through stomatal resistance (Boyer, 1970a; Graziani and Livne, 1971; Moldau, 1973). Mederski, Chen and Curry (1975) have shown that decreases in the net assimilation rates of beans and corn with decreases in water content were totally due to stomatal control.

The pattern of net assimilation rate response to decreasing water potential seems to vary significantly with species. Odening, Strain and

Oechel (1974) have depicted the response of the desert species they studied to increase exponentially as water potential approaches 0 bars. Beadle *et al.* (1973) found that the maximum net assimilation rates of corn and sorghum plateaued over a wide range (-2 to -8 bars) of high water potentials until a threshold was reached below which they decreased rapidly, much as the response of leaf resistance to decreasing water potentials (p. 81). Johnson, Caldwell and Tieszen (1974) have shown net assimilation as decreasing linearly with water potential over the range they examined in arctic species.

Results and Discussion

Leaf Resistance

The mean minimum resistance to water loss by the abaxial surface of *Dryas* leaves at 15°C is 5.6 sec cm ^{1} (Fig. 19). This is higher than the minimum leaf resistances (0.5 to 3 sec cm^{-1}) normally measured for agricultural species and for some arctic species (Stoner and Miller, 1975). It is in the lower half of the range of values measured on temperate shrubs and deciduous trees (Table 10, p. 82). The minimum leaf resistance of *Dryas* is much lower than that measured for most conifers, but it is remarkably similar to the lowest value (4.88 sec cm ^{1}) calculated for leaves of *Dryas* in a similar state on Devon Island by Addison (1973). Ehleringer and Miller (1975) noted that the minimum leaf resistance of some alpine plants increases at temperatures below 15° to 20°C. The leaf resistance of *Dryas* may, therefore, become lower at higher temperatures if the water deficit is not severe. However, since

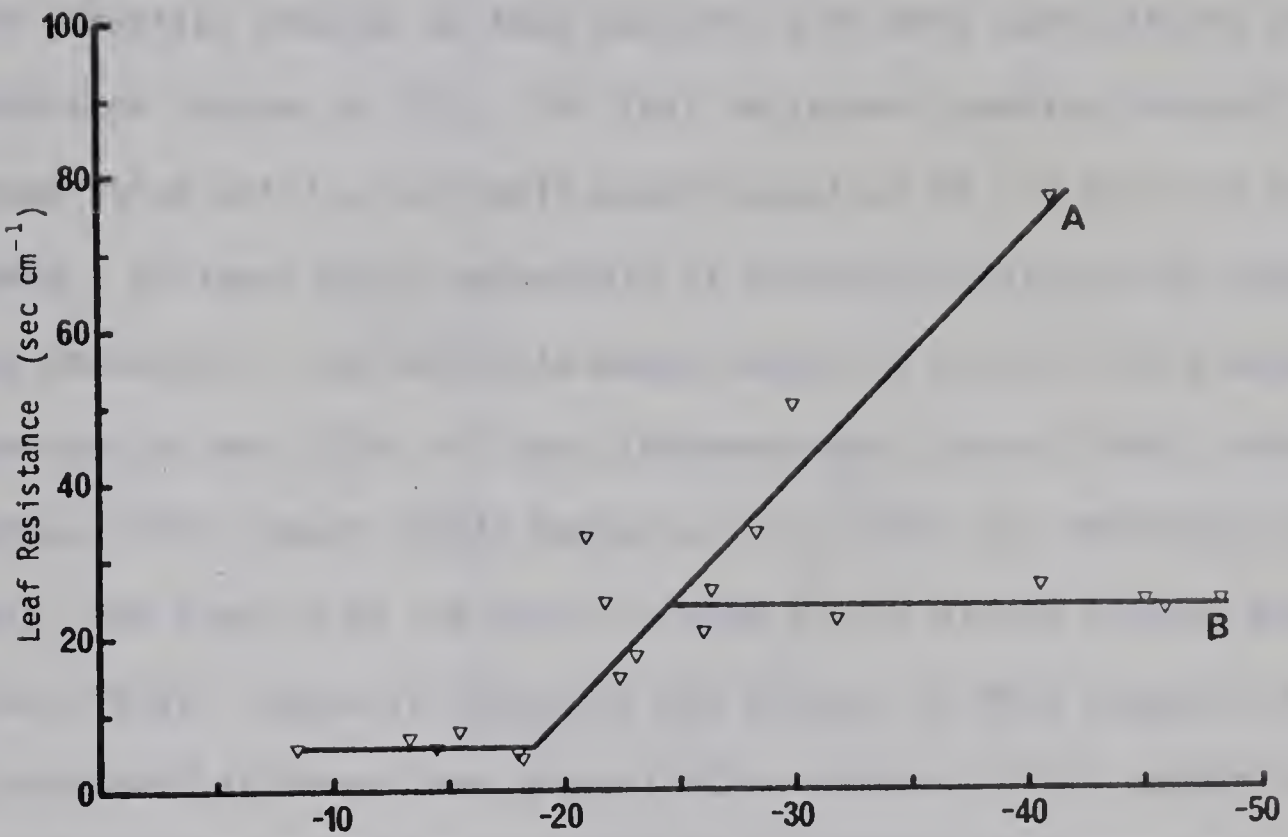
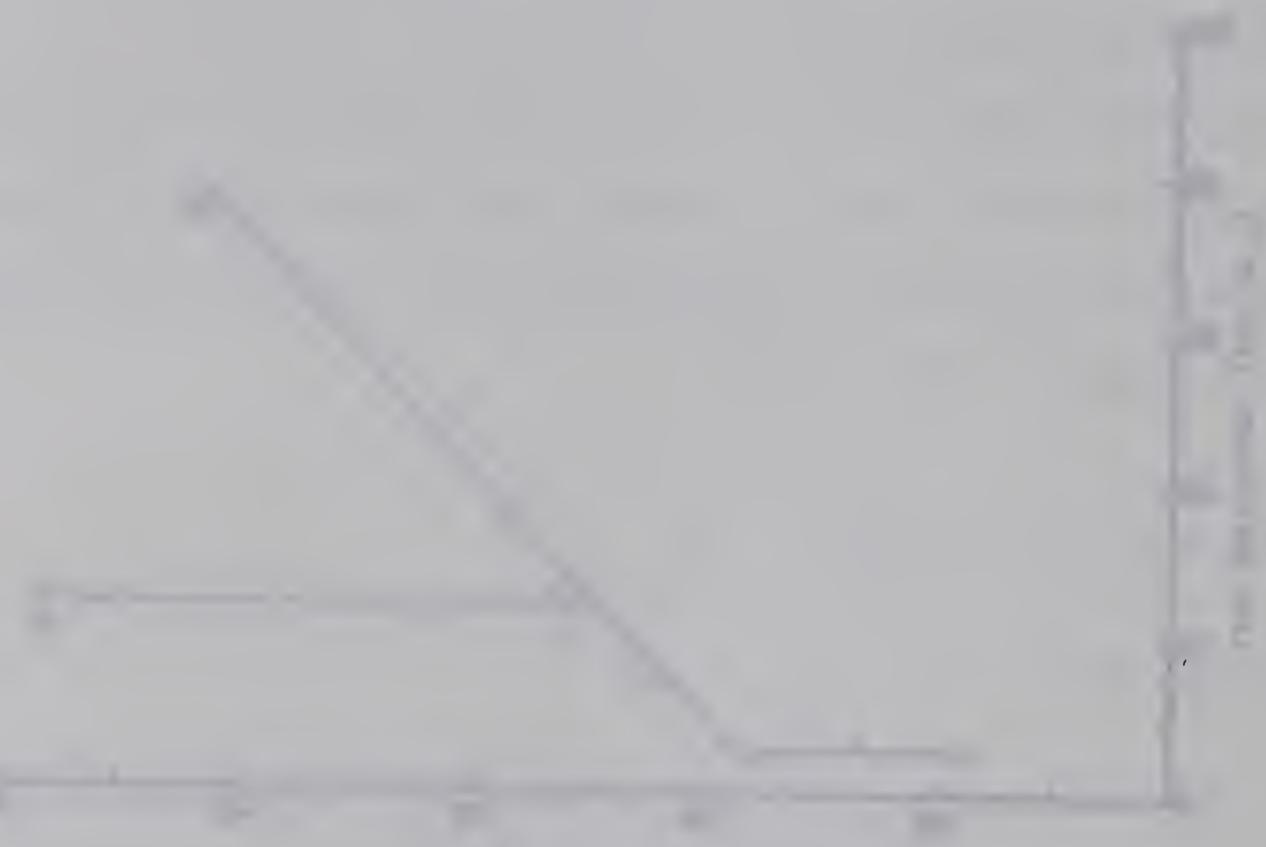


Figure 19. The influence of leaf water potential of *Dryas* on the leaf resistance to water vapour loss as calculated from transpiration rates of detached shoots in potometers. The water potential was altered with mannitol. Light: 200 - 230 $\mu E\ m^{-2} sec^{-1}$; leaf temperature: 15°C; air temperature: 15°C; relative humidity: 42 to 48%. Leaf resistance was calculated for the abaxial surface only.
A: turgor decreases towards 0 bars.
B: turgor is maintained at approximately 4 bars (Fig. 20, p. 87).



leaf temperature on Devon Island on cloudy days is often below 15°C, the higher leaf resistances at low temperatures (15°C) may be more relevant to the situation.

Fig. 19 illustrates a response of leaf resistance to decreasing water potential similar to that observed with many agricultural species (literature review, p. 81). The leaf resistance remains constant at a minimum value until a threshold water potential of -18 bars has been reached. At lower water potentials it increases rapidly with decreasing water potential. The threshold water potential at which this occured in other species was -8 to -17 bars (Kanemasu and Tanner, 1969; Jordan and Ritchie, 1971; Turner, 1974; Beadle *et al.*, 1973) for laboratory grown plants, and from -4 to -14 bars for some arctic plants (Stoner and Miller, 1975). *Dryas* is therefore not unusual in this respect, although its threshold is lower than that of other species. This sudden increase in leaf resistance has been related to a decrease in turgor below a threshold of around 0 to +2 bars (Kanemasu and Tanner, 1969; Turner, 1974; Kassam, 1973) , which possibly corresponds to changes in cell wall elasticity (Gardner and Ehlig, 1965). If this response is related to a threshold turgor in *Dryas*, the shift occurs at a much higher level (+6 to +7 bars, Fig. 20). However, the values of leaf resistance as they vary with turgor are too scattered to justify more than a trend showing increasing resistance with any decrease in the turgor pressure. *Dryas* leaf resistance is therefore more dependent on turgor throughout its range than is that of other species. This may be related to *Dryas'* ability to maintain a constant turgor over a wide range of water potentials. In a situation of moderate water deficit, turgor in meso-

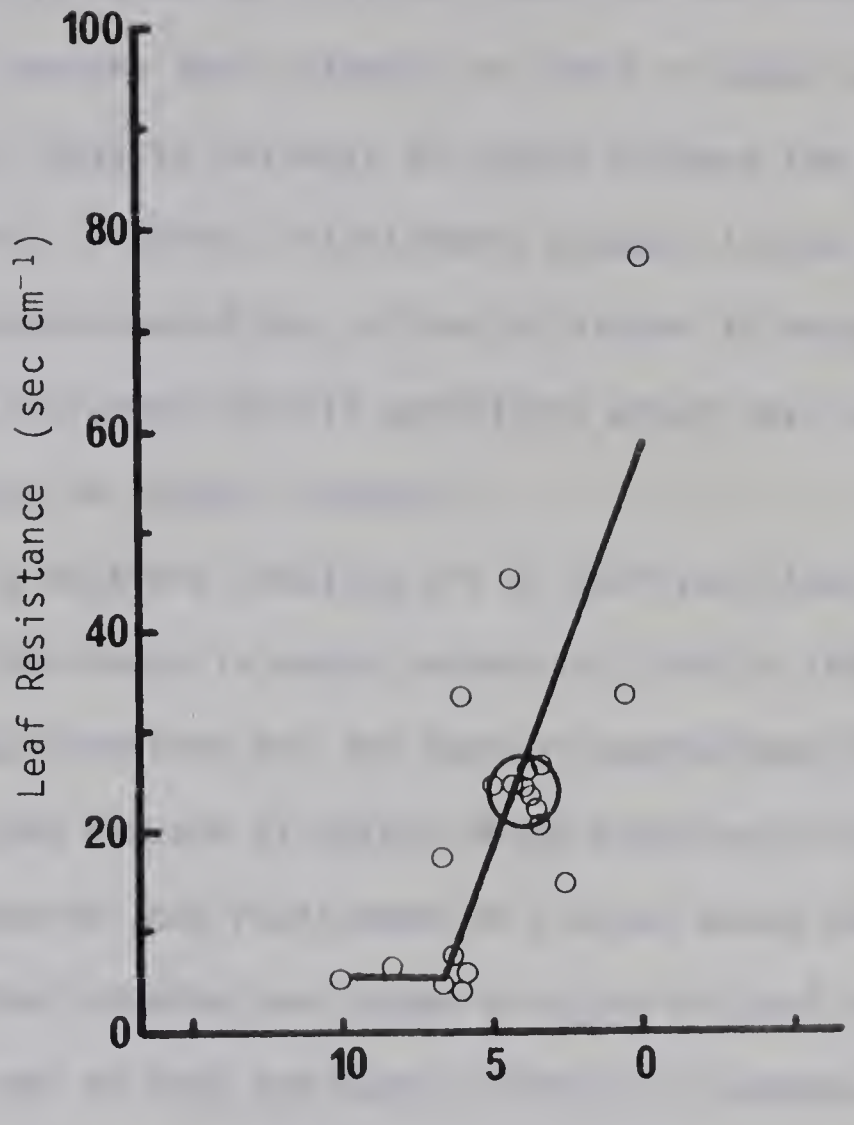


Figure 20. The influence of turgor pressure on the leaf resistance of *Dryas* . Water potential and turgor pressure were altered with mannitol on detached shoots in potometers. The points in the circled area correspond to leaf resistance values of about 24 sec cm^{-1}, which is maintained regardless of the total water potential.

phytic plants will fall below the critical level for an increase in leaf resistance, thereby causing their stomata to close so water can be conserved. In *Dryas*, this is unlikely to happen because the turgor pressure remains high. A direct relationship between turgor at all levels of leaf resistance would thus allow the leaves to have some control over water loss under deficit conditions which may result in only a slight decrease in turgor pressure.

Fig. 19 shows a distinct leveling off of leaf resistance values at 24 sec cm^{1} over a wide range in water potentials (-25 to -48 bars). In every case, the turgor pressure was the same at approximately 4 bars. This can be seen in the cluster of points which have been circled in Fig. 20. This plateau in leaf resistance at a value above the minimum is very unusual. Other studies have shown no signs of leaf resistance reaching a plateau even at very low water potentials (Kanemasu and Tanner, 1969; Troughton, 1969; Stoner and Miller, 1975). It strongly supports the idea that for *Dryas*, the leaf resistance is controlled more specifically by turgor pressure of the leaves than by any other water-related parameter, and emphasizes the need for measurement of component potentials in all future work relating to leaf resistance of non-agricultural species. This response has important implications to the influence of leaf resistance on net assimilation rates because of *Dryas'* ability to maintain a constant turgor over a wide range of water potentials (Fig. 14, p. 73; Fig. 15, p. 75). If *Dryas* leaves maintain a turgor at any level along the line of leaf resistance versus turgor shown in Fig. 20, one would expect the leaf resistance to remain constant at that value, regardless of the leaf water potential, for as long as the

turgor did not change. Addison (1973) reported a leaf resistance value of 20 sec cm^{-1} for *Dryas integrifolia* under relatively dry conditions on Devon Island. This is close to the 24 sec cm^{-1} value at which leaf resistance appeared to plateau in this study.

This experiment was conducted at low light (200 $\mu E\ m^{-2} sec^{-1}$ or 10,000 lux) and temperature (15°C) levels. Changes in these environmental parameters will have an effect on the leaf water status and therefore possibly on the leaf resistance response. Ehleringer and Miller (1975) found minimum leaf resistances to increase at temperatures below 15° to 20°C. The values presented here therefore have more application to evening or cloudy day situations on Devon Island than to the periods of high light intensity which cause high leaf temperatures (Addison, 1973). A much more detailed examination of the response of leaf resistance to all of these parameters would be needed to determine the extent of validity of application of this information to the field situation.

The Influence of Darkness on Leaf Resistance

Dryas stomata are not very light sensitive (Fig. 21). This is especially so at leaf water potentials above -20 bars. Although the differences between leaf resistance in the light and dark were statistically significant (at the 95% level), leaf resistance is much more sensitive to changes in water potential or turgor below the threshold in the light than it is to a change from light to dark. The pattern of response of leaf resistance to water potential in the dark is the same as that in the light. The lack of stomatal sensitivity to darkness is not important to plants growing in continuous light on Devon

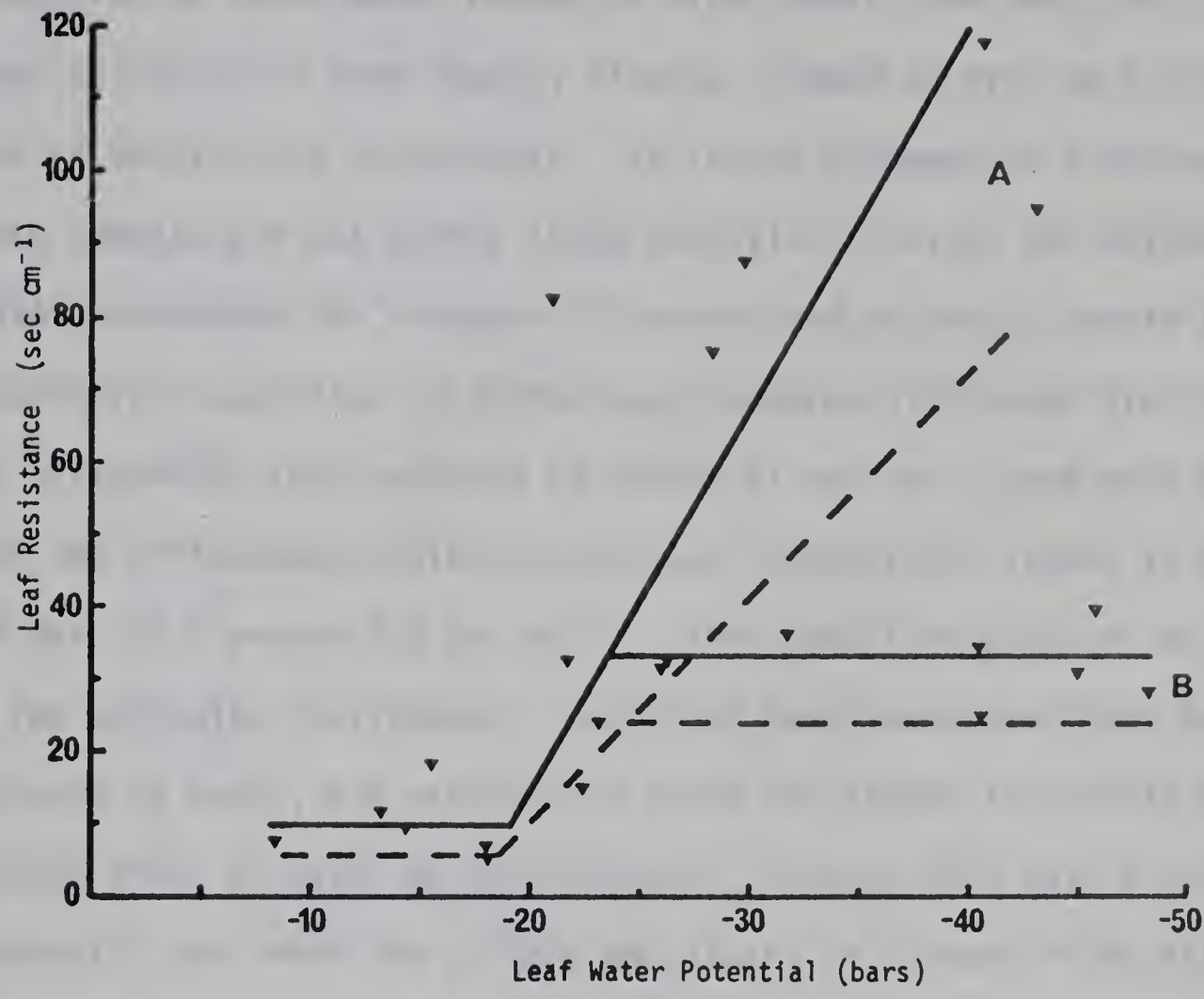
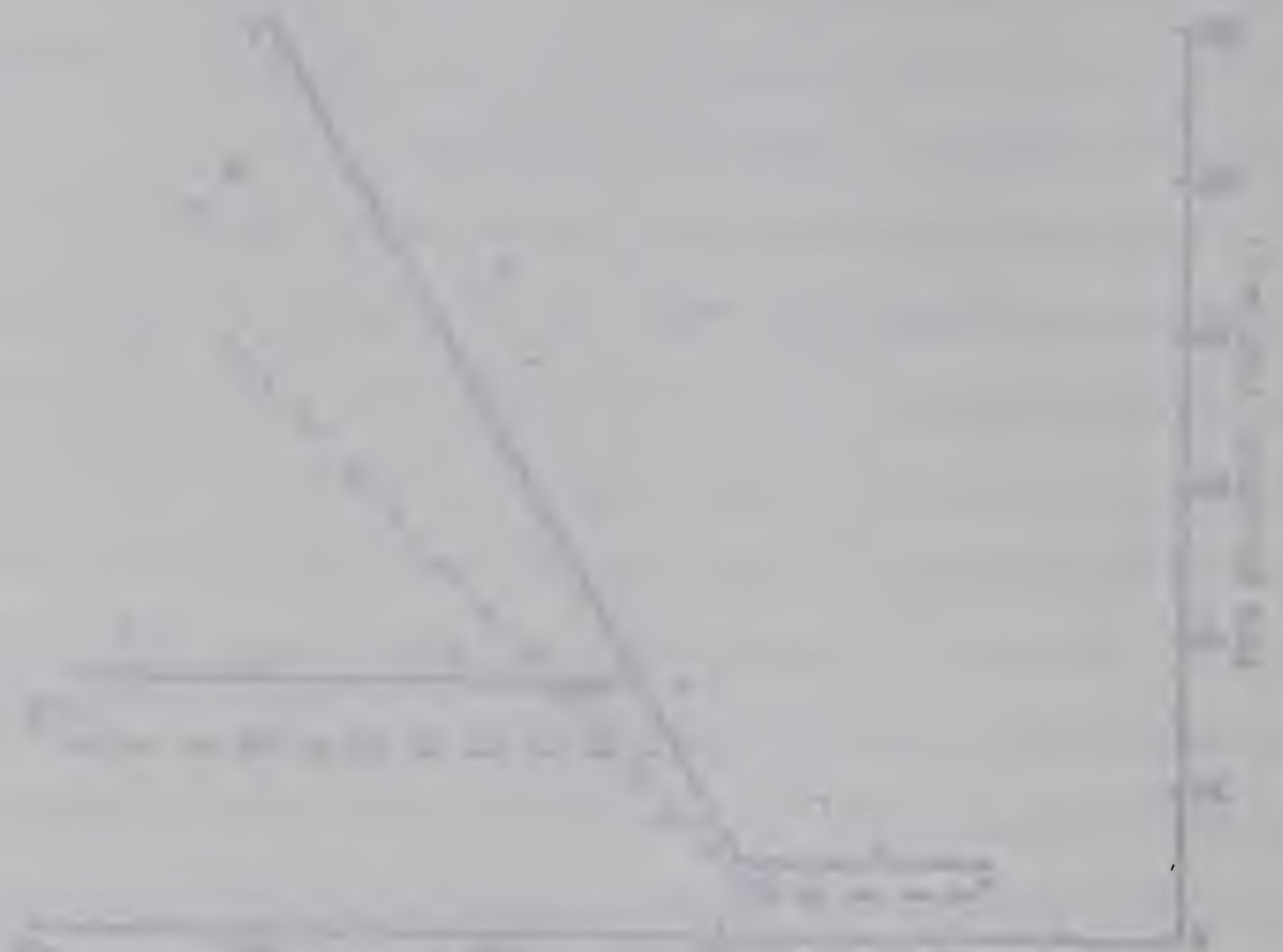


Figure 21. The influence of darkness on the response of *Dryas* leaf resistance to leaf water potential changes. ▼——▼ : response in dark; - - - - : response in light (from Fig. 19, p. 85). Leaf temperature: 15°C; air temperature: 15°C; relative humidity: 42 to 48%.

A: turgor decreases towards 0 bars.
B: turgor is maintained at approximately 4 bars.



Island. It is, however, interesting to note that some preliminary transpiration experiments conducted with shoots from one plant of alpine *Dryas integrifolia* from Jasper, Alberta, showed an even more pronounced lack of sensitivity to darkness. It is not uncommon to find species whose stomata are not highly light sensitive. Davies and Kozlowski (1974) considered the response of *Quercus* and *Fraxinus* stomata to be relatively insensitive to darkness as compared with other tree species. The differences they measured (4 versus 21 sec cm ^{1}) were much greater than the differences exhibited by *Dryas integrifolia* leaves in the light and dark (5.6 versus 9.8 sec cm ^{1}). This condition could be an artifact of low cuticular resistances. Cuticular resistance could not be measured on *Dryas*, but attempts to cause the leaves to hydrate by placing drops of water on their adaxial surfaces were only partially successful even when the cuticle was scored or scraped in an attempt to remove it. This suggests that the cuticular resistance to water loss by *Dryas* is high. The insensitivity of *Dryas integrifolia* stomata to darkness must therefore be real.

The Influence of Water Potential on Net Assimilation

The effect of decreasing water potential on net assimilation rates (Fig. 22) is unusual in that there appears to be an optimum water potential at -9 bars, with decreasing net assimilation rates at higher water potentials. The data presented by Brix (1962) for tomato shows a slight decrease in net assimilation rate at water potentials higher than -2 bars, which may be due to inhibitory effects of very high turgor pressures. The -2 bar optimum is much higher than the -9 bar optimum

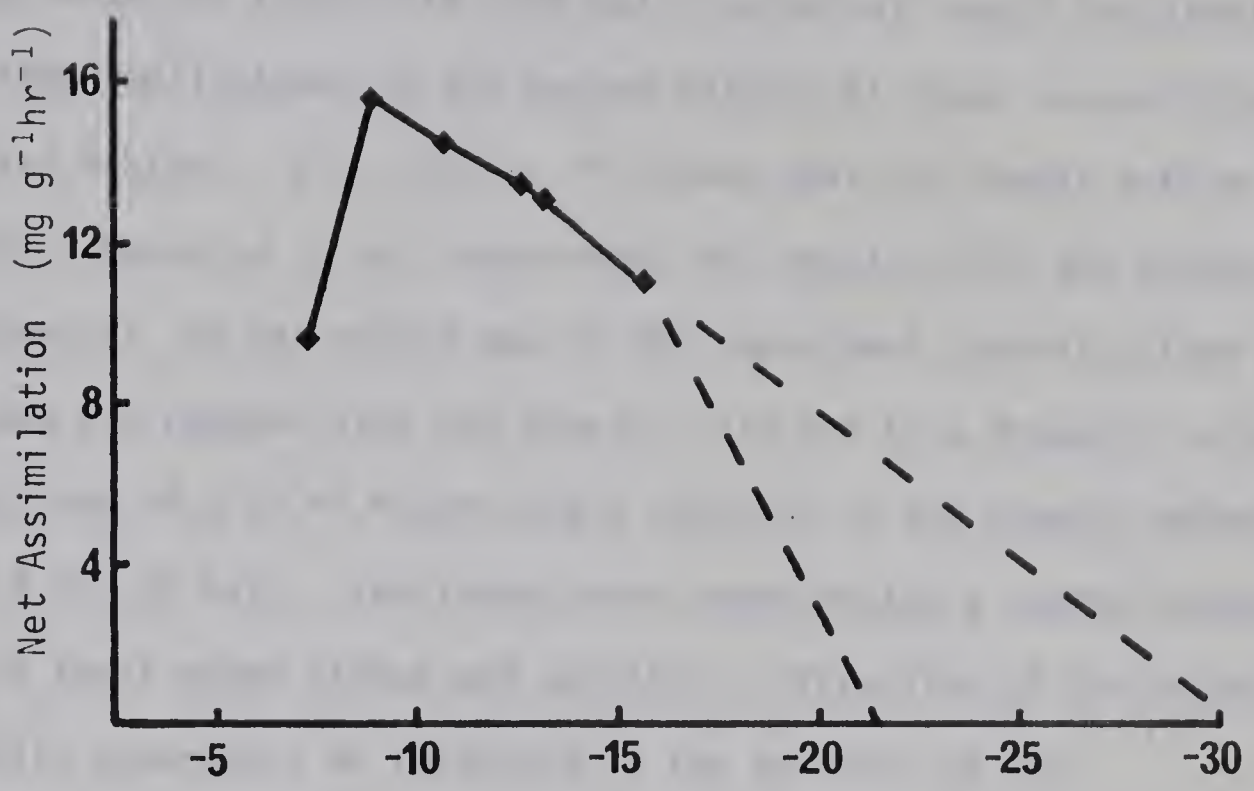


Figure 22. The relationship of net assimilation of CO_2 to leaf water potential in a *Dryas* leaf. The data was collected over a three week period from one mature leaf as the plant dried out. Water potential was measured on adjacent leaves. Leaf temperature: 13.5°C; light intensity: 460 $\mu E\ m^{-2} sec^{-1}$. This data is also presented in Fig. 15a, p. 75. The dashed lines indicate possible trends at water potentials below -16 bars.

for *Dryas* presented here. Net assimilation rates have been shown to increase linearly or exponentially with increasing water potentials and sometimes to plateau above -8 bars (literature review, p. 84). Since water potentials of *Dryas* seldom rise to values above -7 bars, a decrease in net assimilation rates with high water potentials would not likely have serious implications to the carbon balance of *Dryas integrifolia* in its natural habitat. Fig. 15a (p. 75) shows that the lowest rate of net assimilation measured in this experiment was coupled with the highest water potential on the second day of the experiment, shortly after a plastic bag was removed from the plant. This led to a dramatic increase in turgor from +2.5 to +7.6 bars and a decrease in the osmotic potential from -11.6 to -15 bars. The leaves were experiencing a sudden reorganization of their water status and possibly a disruption of the balance of metabolic processes, as reflected in the low rate of net assimilation for that day. For this reason, the response depicted for water potentials greater than -8 bars in Fig. 22 should be regarded with some doubt. If the data point at the highest water potential is eliminated, net assimilation appears to decrease almost linearly with water potential as shown by Johnson *et al.* (1974), with a tendency toward a plateau at water potentials greater than -8 bars as shown by Beadle *et al.* (1973). The maximum net assimilation rate observed in this experiment (15.2 mg $g^{-1}hr^{-1}$) approaches the mean maximum rate (18.7 mg $g^{-1}hr^{-1}$) measured in the temperature response experiments (p. 25). Therefore, the possibility that this response will plateau at higher water potential values is good.

There are some other interesting aspects of this effect of water

potential as it relates to *Dryas'* net assimilation of carbon. The net assimilation rate is optimum at a water potential (-9 bars) which is close to the values for the lower limit for the maximum net assimilation plateau observed for agricultural species (Beadle *et al.*, 1973; Boyer, 1970a; Brix, 1962; Table 11). The net assimilation rates of most of the species listed in Table 11 drop to 50% of the maximum at water potentials of -10 to -16 bars. At -15 bars, *Dryas* is still assimilating at 70% of its maximum rate (Fig. 22, p. 92). *Dryas integrifolia* therefore has an ability to maintain net carbon assimilation at significant rates at water potentials below those which would severely limit such activity in mesophytic temperate species. The response of the rate of net assimilation of *Dryas* to water potential is similar to that observed for arctic species (Johnson *et al.*, 1974) and for the xerophytic *Larrea* (Odening *et al.*, 1974).

The pattern of change of leaf resistance with water potential (Fig. 19, p. 85) must exert some influence on the capacity of *Dryas* to assimilate carbon positively under field conditions. Fig. 22 (p. 92) shows that net assimilation rates decrease slowly at water potentials below -8 bars. There is no data following this trend below -16 bars. If the leaf resistance in the field does increase rapidly at water potentials below -18 bars, this would result in a marked decrease in net assimilation rates at this level. One can therefore predict that the possible net assimilation of carbon at water potentials less than -20 bars should be negligible. Jordan and Ritchie (1971) observed a much lower threshold of water potential required to effect the increase in leaf resistance in field grown plants than in laboratory grown

Table 11. Water potentials of various species at maximum rates of net assimilation and at 50% and 0% of the maximum rate.

Species	Water potential (bars)			Reference
	100% NA	50% NA	0% NA	
Loblolly pine	≥ -5		-11	Brix, 1962
Tomato	-6.5	-10	-14.5	" "
Sorghum	-2 to -8	-10		Beadle *et al.*, 1973
Corn	-2 to -8	-12		" "
Corn	-3.5	-13	< -16	Boyer, 1970a
Sunflower	-7 to -8	-15	< -18	Boyer, 1970b
Saxifraga			-25	Teeri, 1973
Chilopsis	> -1	-15	-35	Odening *et al.*, 1974
Encelia	> -1	-15	-46	" "
Soybean	-11	-16	< -24	Boyer, 1970a
Geum rossii	≥ -7	-18	(-28)*	Johnson *et al.*, 1974
Deschampsia	≥ -9	-23	(-38)*	" "
Kobresia	≥ -12	< -24		" "
Larrea	≥ -10	-27	-75	Odening *et al.*, 1974
Artemesia			< -92	Kappen *et al.*, 1972

* projected values

plants (-30 bars versus -16 bars). Ehleringer and Miller (1975) also showed that leaf resistance remained low at lower water potentials in plants growing in dry sites as compared with those grown in wet sites. This suggests a possible acclimation to environmental conditions. If this happened in *Dryas*, it would be difficult to predict at which point of water potential the leaf resistance would become a critical factor in limiting net assimilation rates.

The decrease in net assimilation rate at water potentials above the threshold for increasing leaf resistance, suggests that water status must have an effect on photosynthesis other than through leaf resistance.

The ability of *Dryas* to assimilate carbon positively at relatively low water potentials is necessary to its survival on Devon Island because the plants often experience such conditions. However, if the data in Fig. 22 (p. 92) is projected to lower water potentials, the net assimilation rate should approach zero at water potentials between -20 and -30 bars. Such water potentials were often measured on Devon Island (Addison, 1973). The theory, presented earlier (p. 28), that water status may be a significant factor in explaining the discrepancy between the rates of net assimilation measured in the field and those measured under controlled conditions, is therefore valid. This data suggests that the growth of *Dryas integrifolia*, as related to its carbon balance, must be severely water limited on the beach ridges of Devon Island.

CONCLUSIONS AND ECOLOGICAL IMPLICATIONS

Dryas integrifolia on Devon Island is subjected to some extreme environmental conditions, including very high (35°C) and low (near 0°C) leaf temperatures, long periods of low light interspersed with brief periods of bright sunlight, and a severe water shortage in its gravel beach ridge substrate (Addison, 1973; Mayo *et al.*, 1973). The examination of the response of net assimilation by single leaves of this species to varying controlled environmental conditions has led to some insights into how *Dryas* is able to maintain itself and grow in such a habitat.

The net assimilation rate of *Dryas* is optimum at 9° to 14°C. At this temperature, the photosynthetic system is very responsive to changes in light intensity, with a low light compensation point (22.4 $\mu E\ m^{-2}sec^{-1}$) and a rapid rise to a high rate of net assimilation (18.7 $mg\ g^{-1}hr^{1}$) at light saturation (Fig. 23). At even lower temperatures (0°C) net assimilation of CO_2 is still very responsive to changes in light, which is especially apparent in its extremely low light compensation point (11.6 $\mu E\ m^{2}sec^{1}$). This characteristic could be advantageous in the low light and leaf temperature conditions prevalent on Devon Island in the evenings and during the long periods of overcast skies. It was under such conditions that the highest rates of net assimilation were observed for whole plants in the field (Mayo *et al.*, 1973; Thompson *et al.*, 1973).

The age of mature leaves is not an important factor in limiting the

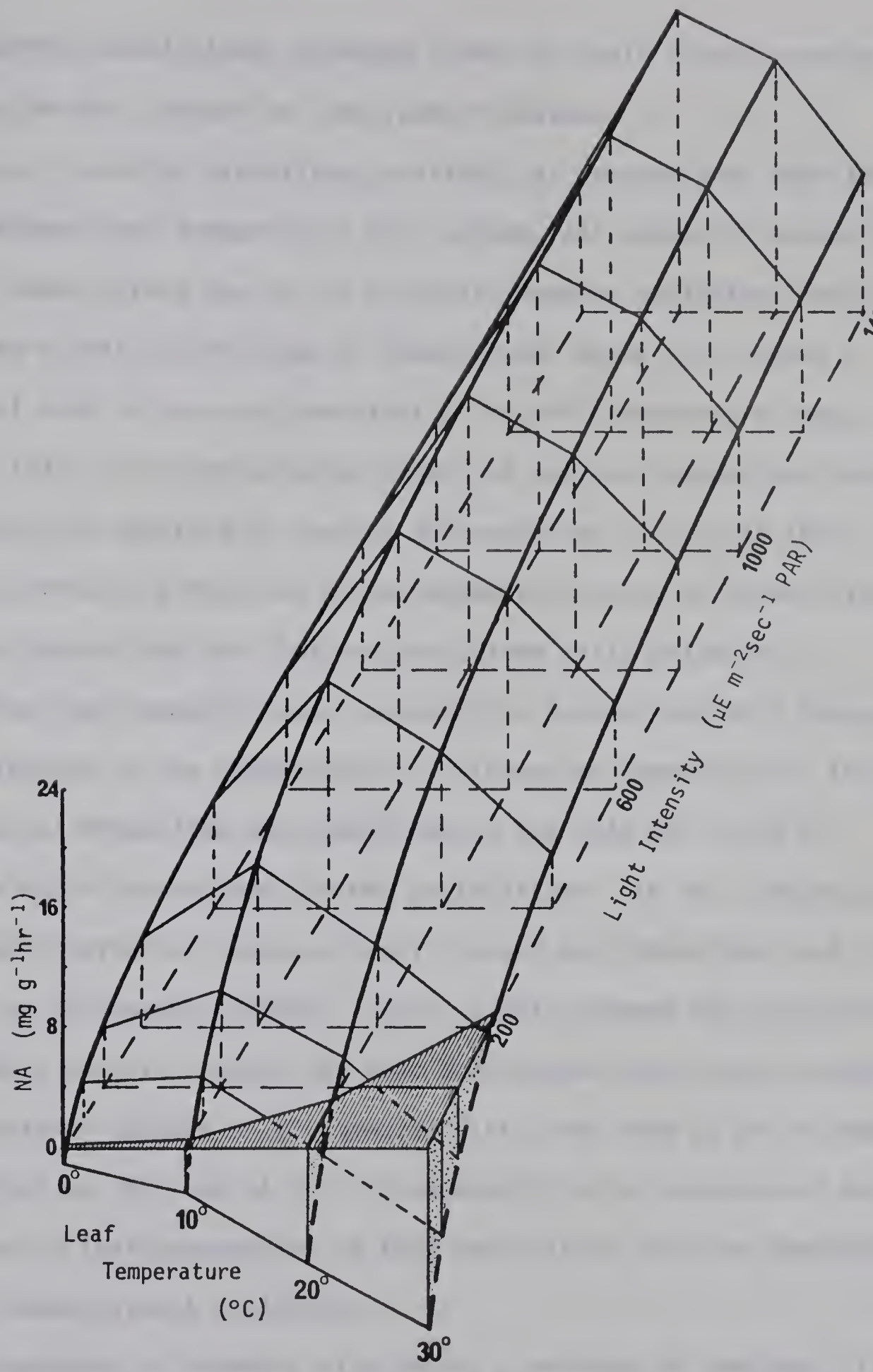


Figure 23. The interrelationship of the influences of leaf temperature and light intensity on the rate of net assimilation (NA) by single leaves of *Dryas integrifolia*.

rate of carbon assimilation, although leaves in their second growing season may be more productive than younger leaves.

Dryas is able to assimilate positively at temperatures down to -5°C. Although leaf temperatures will seldom fall below 0°C during the summer on Devon Island due to the constant incoming radiation, increases in the rate of net assimilation at temperatures above -5°C ensure a substantial rate in the more prevalent 0° to +5°C temperature range (Courtin, 1973). An adverse after-effect of subzero temperatures on net assimilation was observed to cause a 35% reduction in rate at 10°C. This should not normally affect the carbon balance of *Dryas* on Devon Island in the summer because the leaf temperature seldom falls below 0°C

Active (non-dormant) *Dryas integrifolia* leaves have high rates of dark respiration at low temperatures. This may be important for the maintenance of metabolism and growth during the cold (0° to 15°C) conditions which are optimum for net assimilation. In this temperature range, photorespiration rates are very low and must therefore have little influence on the carbon balance. *Dryas* is well adapted for conservation of its carbon reserves during the long dark autumn and winter periods. This is achieved through a 10°C upward shift (the rate at 0°C in summer is equivalent to the rate at 10°C in dormancy) in the response of dark respiration to leaf temperature so that respiration rates at temperatures below 0°C become almost negligible.

The approach of dormancy also causes a decrease in the rate of net assimilation. This may be due to a feedback inhibition by a build up of carbohydrates caused by the decreasing rate of respiration, or it may be related to the decrease in total and component water potentials

observed in conjunction with approaching dormancy.

Dryas shows a strong resistance to increasing its leaf water potential above -7 bars. This may be related to a maintenance of frost hardiness during the summer. The marked decrease in water potential as dormancy is approached may be related to increased frost hardiness in preparation for severe cold during the winter.

Dryas leaves have a marked ability to maintain a high and constant turgor over a wide range of water potentials and water contents in their active "summer" state. This ability suggests that *Dryas* cells must have elastic walls, which is unusual for xerophytic species (Jarvis and Jarvis, 1963). Changes in leaf resistance are dependent on turgor pressure rather than on total water potential. Since *Dryas* is exposed to severe soil drought during much of its growing season, this ability to maintain turgor may be important for continued growth as related to cell expansion and carbon assimilation.

Net assimilation rates decrease at water potentials below -9 bars, regardless of the turgor pressure, and have been projected to reach compensation between -20 and -30 bars. Although this response may be shifted to lower values in the more xeric-adapted field grown plants, it points to the importance of a favourable water status to net assimilation. Given the growing conditions on Devon Island with long periods of low light and temperature which the net assimilation system seems to have adapted to utilize optimally, and with the generally low leaf water potentials (less than -20 bars, Addison, 1973), this study indicates that water deficit must be the overriding limiting factor to net assimilation and to growth of *Dryas integrifolia* on Devon Island.

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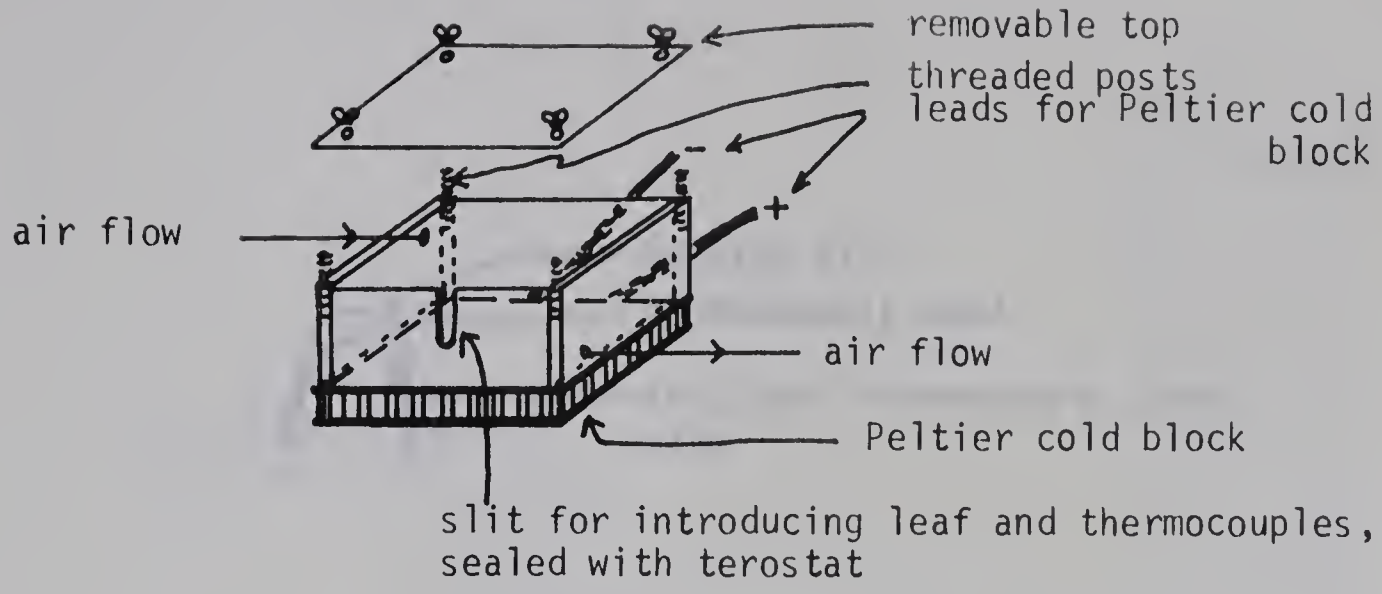
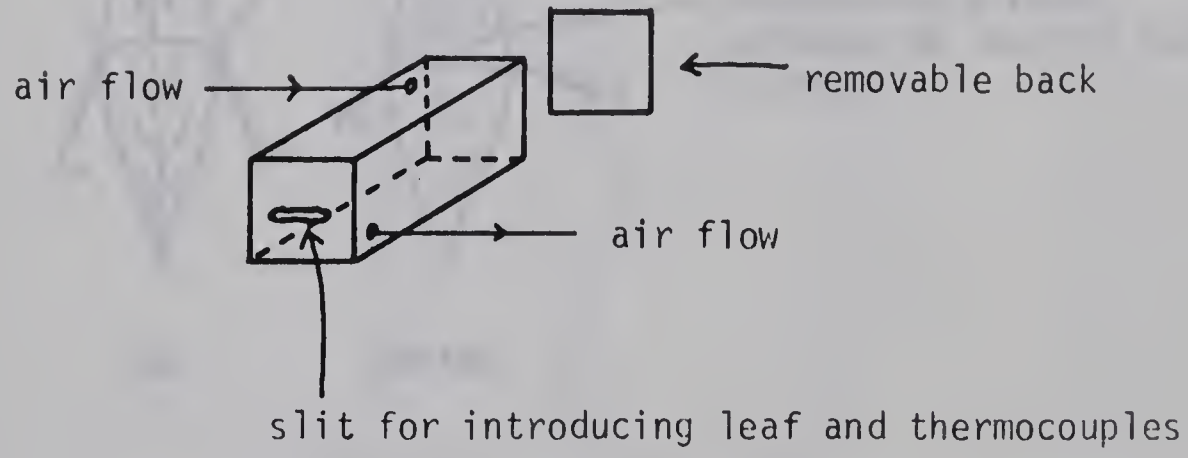
Appendix A. Diagrams of cuvettes, leaf thermocouples and the flow chart for the infrared gas analysis system.

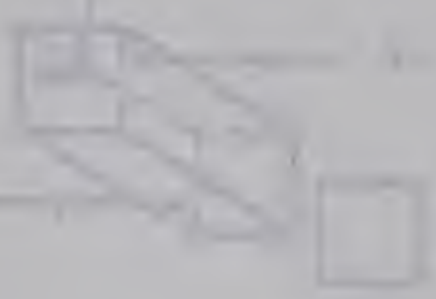


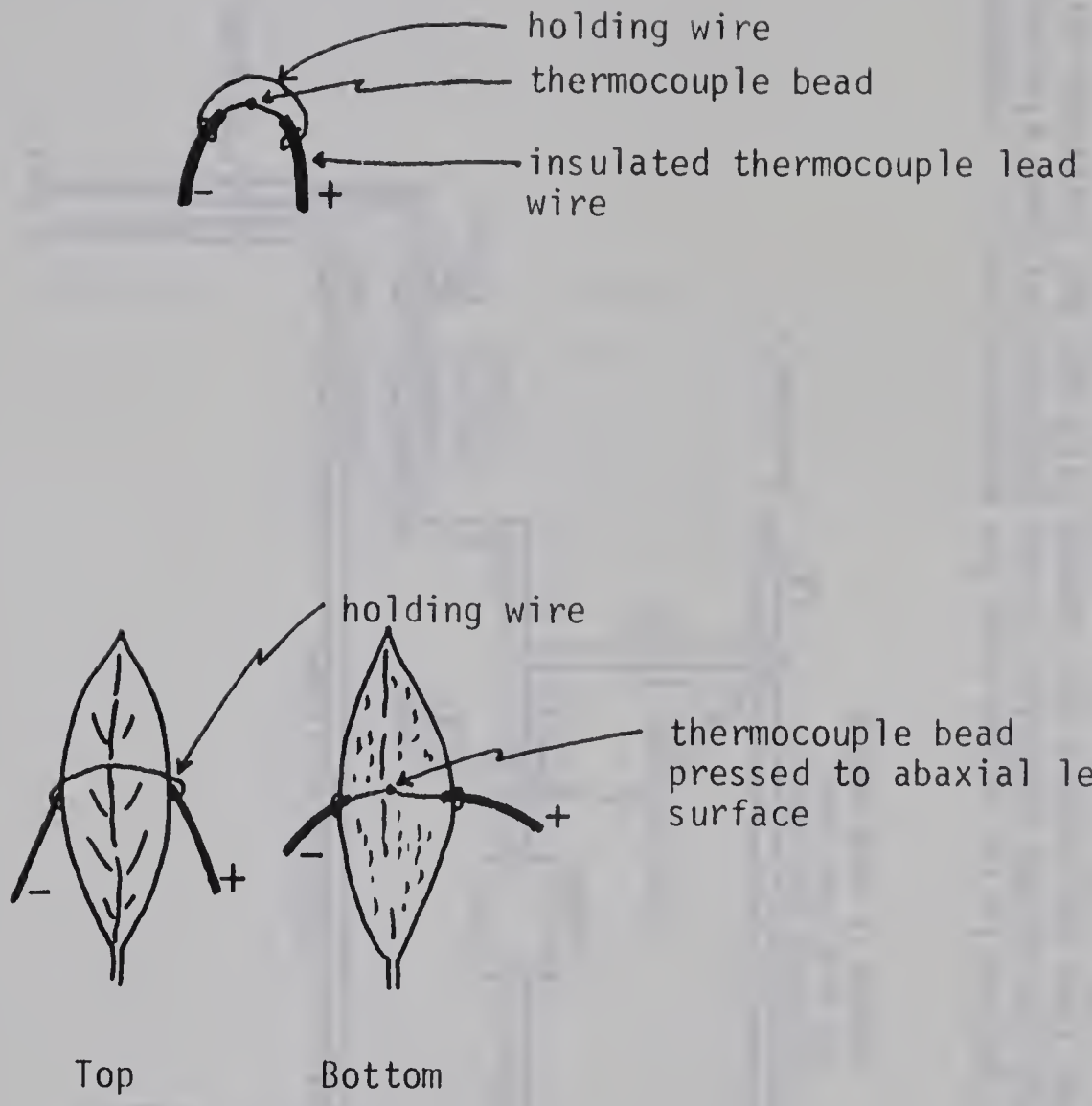
a) first cuvette, with internal cooling unit.



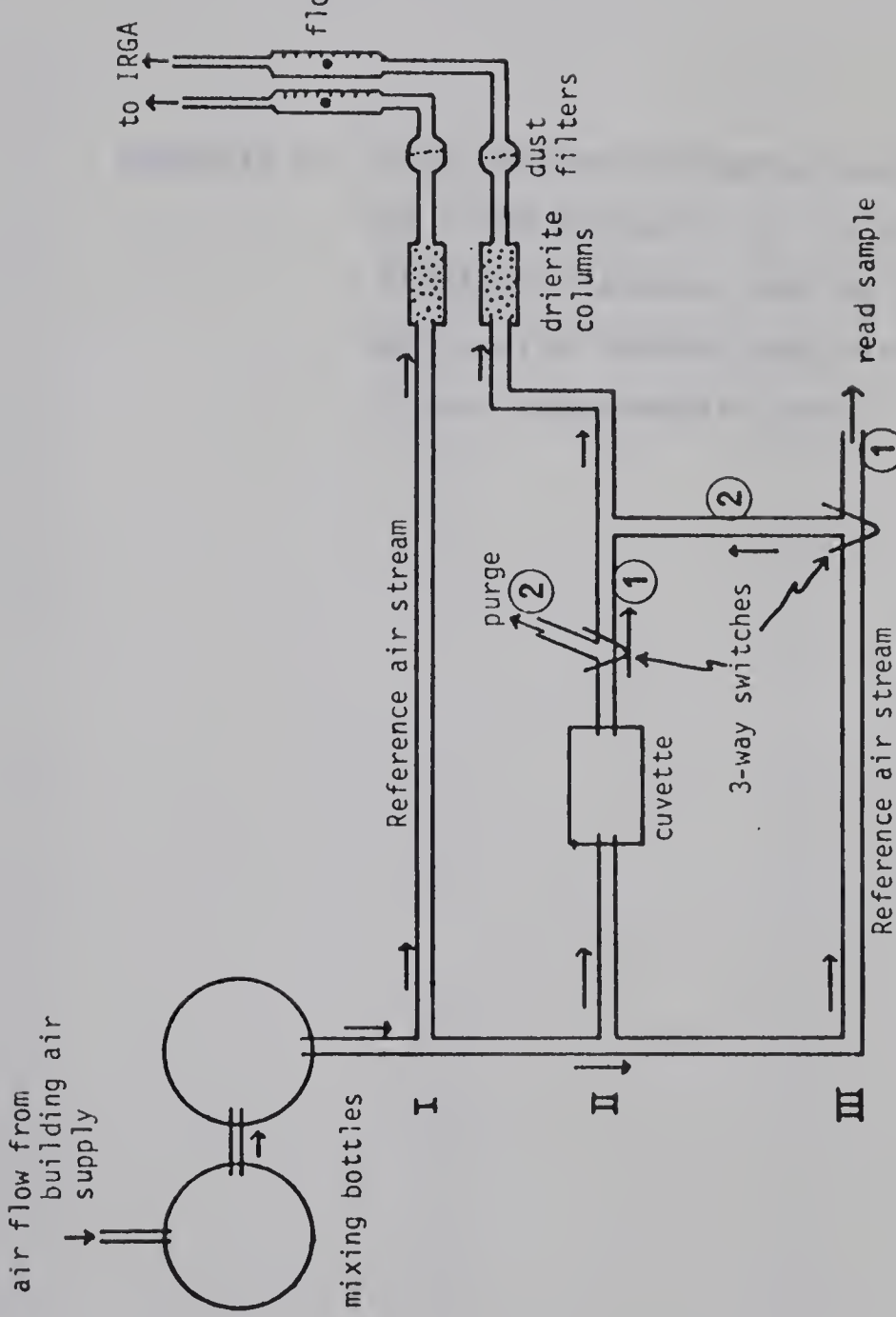
b) second cuvette, without cooling unit.

Diagrams of the cuvettes used to measure net assimilation by single leaves of *Dryas*.

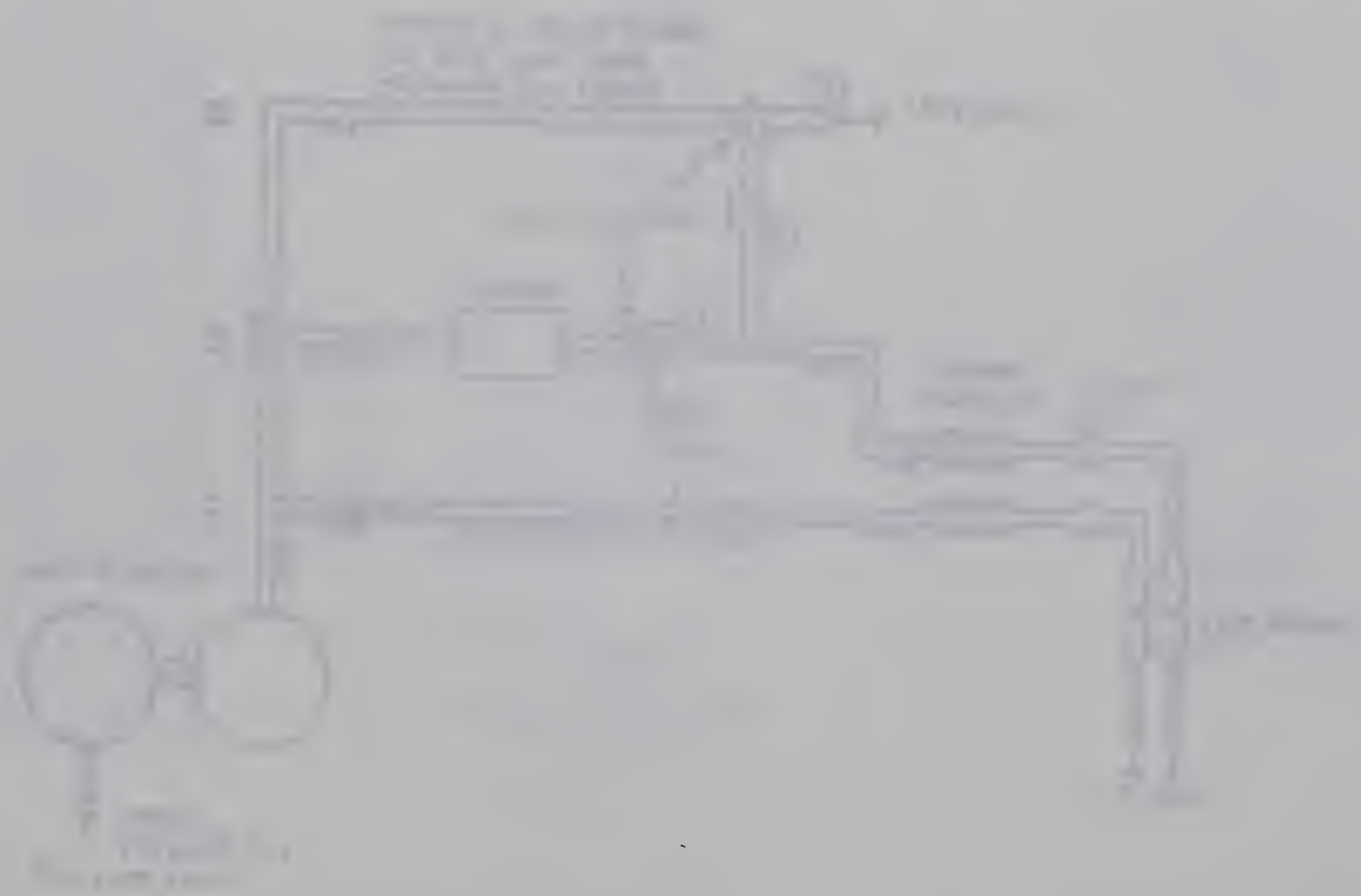




Method of attachment of a thermocouple to the leaf. The leaf is sandwiched in between the thermocouple lead wires and the bead (5 mil copper-constantan) on its abaxial surface, and a thin holding wire on its adaxial surface. These are pressed lightly together with forceps so that the bead will retain a position in close contact with the leaf.



A flow diagram of the gas analysis system used for measuring net CO_2 exchange of a leaf. The leaf is inserted in the cuvette. 3-way solenoid switches alternate the air flowing to the IRGA from the sample air stream (II) and the reference air stream for a zero line (III) at 15 or 20 minute intervals. Air flows through the reference air stream (I) to the IRGA in both cases. Air flows through pathways marked 1 when sample (cuvette) air is being analyzed, and through pathways marked 2 when the zero line is being recorded.



Appendix B. ISCO spectroradiometer analysis of the quality of light produced by the standard growth chamber lighting fixtures, and by the mercury vapour lamp and quartz-iodide lamp used to supplement these in the experimental work.

An analysis of the quality of light produced by the various sources of illumination used in the experimental work. The ISCO spectroradiometer was used .

Wavelength (nm)	Intensity of irradiance ($\mu W\ cm^{-2} nm^{-1}$)		
	Growth chamber* lamps at 30"	Mercury vapour lamp at 4"	Quartz-iodide lamp at 18"
380	0.4	4.	1.5
400	4.2	23.1	2.3
425	10.1	25.	2.5
450	13.2	40.8	5.3
475	11.9	6.1	7.1
500	11.3	10.6	8.9
525	12.5	9.9	10.6
550	19.3	242.6	12.6
575	21.7	168.2	15.1
600	19.3	49.8	17.6
625	11.6	46.6	19.9
650	5.7	84.3	21.7
675	2.9	98.2	23.6
700	2.1	30.2	24.9
725	1.2	15.3	25.6
750	1.2	10.4	24.6
800	0.8	9.2	28.1
850	0.6	9.1	28.4
900	0.2	9.0	25.6
950	0.2	9.5	17.7
1000	0.9	25.9	11.8
1050	1.	21.5	16.9
1100	0.1	9.1	18.
1150	0.5	15.3	10.7
1200	0.7	8.3	3.1
1250	0.8	6.4	3.
1300	0.03	4.8	2.7
1350	0.13	7.7	0.5
1400	0.2	9.2	0.4
1450	0.04	4.1	0.1
1500	0.1	3.9	0.1
1550	0.2	4.7	0.1

* combined warm white fluorescent and 100 watt incandescent lamps.

Appendix C. Light response characteristics of net assimilation by arctic and alpine plants.

Light response characteristics of net assimilation by arctic and alpine plants.

Species	Compensation point ft-c	Saturation point ft-c	Temperature °C	Reference
Chamaenerium latifolium	150	1500	20°	Müller, 1928
Salix glauca	150	≥ 1200	20°	"
Ranunculus glacialis	200	1700	20°	Wager, 1941
Saxifraga cernua	250	1300	20°	"
Oxyria digyna	300	2800	25°	"
" "	250-300	2000-5000	20°	Mooney and Billings, 1961
Dryas punctata		2000-3000	18°	Gerasimenko and Zalensky, 1973
Carex bigelowii (spring)	400-500	2400-3000	20°	Hadley and Bliss, 1964
Juncus (spring)	"	"	20°	"
Potentilla (spring)		2000-2400	20°	"
Arctophila fulva, Alopecurus alpinus, Arctagrostis latifolia, Calamagrostis holmii, Poa malacantha, Poa arctica, Dupontia fischeri	≤ 125	≤ 5000	15°	Tieszen, 1973
Hierochloë alpina	250	5000	15°	"
Elymus arenarius	< 125	> 5000	15°	"
Geum (spring)	300	7000-9000	20°	Hadley and Bliss, 1964
Thalictrum	150-300	7000-9000	20°	Mooney and Johnson, 1965
Celmisia, Chionochloa	550		20°	Scott, Menalda and Rowley, 1970
Dryas integrifolia	510	9000	20°	this study